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CATALOGUE

OF THE

CHAETOPODA

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(NATURAL HISTORY).

A. POLYCHAETA:

PART I.—ARENICOLIDAE.

BY

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PREFACE

THE present work, which was undertaken at the suggestion of the former Director, Sir E. Ray Lankester, K.C.B., F.R.S., covers but a small proportion of the ground to be gone over in making a Catalogue of the Chaetopoda or even of the Polychaeta.

Although the volume appears as "Part I" of a more general catalogue, its selection for the first place was a fortuitous circumstance, depending on the fact that Dr. J. H. Ashworth, the author, had already devoted special attention to the Arenicolidae when the idea was first projected. The Family in question was thus not chosen because it was supposed to come naturally at the beginning. But as circumstances have placed it there, it has been thought advisable to devote some pages to an introductory survey of the history and classification of the Chaetopoda, and in particular of the Polychaeta. Morphological characters are largely employed by the author in characterising the species.

Mr. F. Jeffrey Bell, whose official duties in the Museum include the care of the specimens of Chaetopoda, has devoted much time to the editing of this Volume.

The continuation of the series of volumes on Chaetopoda is not at present provided for, but it is hoped that opportunities will present themselves from time to time of continuing the series which has been begun by Dr. Ashworth.

SIDNEY F. HARMER,
Keeper of Zoology.

BRITISH MUSEUM (NATURAL HISTORY),
LONDON, S.W.,
November, 1912.

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INTRODUCTION

The family Arenicolidae, though small in the number of its genera and species, holds an important place in the literature of Polychaeta. One of the members of this family—*Arenicola marina*, the common lugworm—is the most abundant and most readily accessible Polychaete of northern and western Europe. Probably no other marine worm has been so frequently observed, collected and dissected, and, consequently, the records and descriptions of which it is the subject form a very extensive series. Twenty years ago the anatomy of the other species of *Arenicola* was almost unknown; the accounts of the internal organs, given in descriptions of the genus *Arenicola*, referred only to *A. marina*, and it seemed to be taken for granted that all the other species agreed in structure with this. Several of the internal organs, notably the statocysts, oesophageal caeca, nephridia and septal pouches have, however, been found to exhibit well-marked differences, in form or number, in the various species, and to afford considerable help in systematic work. In preparing the diagnoses, I have made full use of the internal characters, the value of which will be especially appreciated in those cases where it is necessary to determine defectively preserved or incomplete examples, which, as experience has shown, can seldom be diagnosed safely by examination of their few and imperfect external features. By means of the keys and diagnoses provided, the identification of the members of the family Arenicolidae will, it is hoped, be accomplished with certainty and with comparative ease.

Questions of synonymy have received careful consideration and full treatment in the text. I have examined all the extant types of the species of *Arenicola*, and, in the case of those species the types of which are no longer preserved, I have analysed the published descriptions, and have compared them with the long series of specimens at my disposal, with the result that I can confidently state my conviction that all the known forms fall into the eight species described in this Catalogue.

In addition to the British Museum Collection, the entire

Collections of *Arenicola* in the Museums of Berlin, Paris, Cambridge (Mass.) and the Smithsonian Institution, together with interesting examples from the Museums of Copenhagen, Dublin, Hamburg, Reykjavik, St. Petersburg, Stockholm and Vienna, have been sent to me for examination. I am much indebted to the authorities of these institutions for placing their material at my disposal. During the last twelve years I have collected, and many friends have generously sent to me, large numbers of specimens of *Arenicola*, in various stages of growth, selected examples of which have recently been added to the British Museum Collection. The possession of this abundant material has enabled me to revise and extend previous work upon the characters used in diagnosis, and to ascertain their range of variation. In addition to the acknowledgments made in the text, I am glad to have this opportunity of tendering my sincere thanks to the following friends, who have aided my work by the gift or loan of specimens: Prof. W. B. Benham, F.R.S., Prof. H. C. Bumpus, Geheimrat Prof. Dr. E. Ehlers, Prof. P. Fauvel, Prof. J. D. F. Gilchrist, Prof. W. A. Haswell, F.R.S., Prof. Harold Heath, Prof. A. D. Howard, Dr. R. S. Lillie, Prof. F. Mesnil, Mr. R. Southern, and the Directors of the Marine Laboratories at Alexandrowsk (Gouv. Archangelsk), Cette, Millport, Plymouth, Santander, Sevastopol and Trieste.

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University of Edinburgh.

September 23, 1912.

CATALOGUE

OF THE

ARENICOLIDAE.

HISTORICAL ACCOUNT OF THE CHAETOPODA, WITH SPECIAL REFERENCE TO THE POLYCHAETA AND THEIR CLASSIFICATION.

Naturalists as remote as Aristotle were acquainted with Chaetopoda and other worms, the records of which thus extend backwards to the earliest works on natural history. The chief object of the historical account given in the following pages is to trace the principal stages in the growth of knowledge regarding the Chaetopoda, especially the Polychaeta and their classification, and to indicate in the different schemes of classification proposed the position of the worms which form the subject of the present Catalogue.

Aristotle recorded in his "Historia Animalium" the occurrence of marine scolopendrae,[1] similar to their terrestrial congeners but somewhat smaller, redder in colour, and having a larger number of more slender feet. He stated that these animals are to be found in the neighbourhood of rocks, and that they do not occur in very deep water. The animals referred to were probably nereidiform worms. Aristotle also mentioned helminthes or intestinal worms. Pedacius Dioscorides[2] described the use in medicine of *Scolopendra marina*, earthworms and leeches.

Allusions to marine scolopendrae occur in the writings of Pliny[3] and Aelianus,[4] and the former also referred to *Hirudo* and *Lumbricus*.

[1] Lib. ii, cap. xiv, 2. σκολόπενδραι θαλάττιαι.

[2] De Materia Medica [written probably about 60 A.D.]. Recens. C. Sprengel, Lipsiae (1829), pp. 174, 195, 708, 709.

[3] Nat. Hist., Lib. ix, cap. lxvii, 3 [about 78 A.D.].

[4] De Natura Animal., Lib. vii, cap. xxvi [about 220 A.D.].

To Pliny and his contemporaries, and to his successors during the next sixteen centuries, the names *Hirudo* and *Lumbricus*[1] had a much wider significance than they have at the present day; these writers included leeches of all kinds under the name *Hirudo*, and they applied the designation *Lumbricus* to intestinal worms or to earthworms,[2] or so used it as to include both.

From the time of Pliny onwards for more than a thousand years little real advance was made in regard to the knowledge of worms. During this period various authors repeated, wholly or in part, the accounts of Aristotle and Pliny, sometimes with fanciful embellishments, but, for the most part, they added little or nothing new. Most of the references to worms in these old writings relate to parasitic worms, leeches and earthworms, and especially to the medicinal use of the two latter. The treatise "De Animalibus" in he works of Isidorus, Bishop of Seville (560–636 A.D.), is noteworthy for a chapter[3]—"De Vermibus"—under which heading are included *Sanguisuga* [leeches], parasitic worms ("Vermes carnium"), namely, *Lumbricus*, Ascaridae, etc., and also *Multipes* [centipedes],[4] *Scorpio*, *Limax*, *Bombyx*, *Teredo*, etc. Isidorus placed the Vermes next the snakes, but took care to point out the fundamental distinction between them, that is, that the former are without a backbone—"non est illi spinae rigor."

Albertus Magnus' (1193–1280) "De Animalibus" contains brief notes, based chiefly on the works of previous writers, especially Pliny, on the marine scolopendra, *Seta* [*i.e. Gordius*], *Sanguisuga* and *Lumbricus*.

Edward Wotton[5] (1552) gave a clearly written digest of previous works, but added little new information; in his description of fishes reference is made to leeches and, in the chapter on "Insects," to *Scolopendra marina*, *Intestina terrae* [*i.e.* earthworms], Ascaridae and other parasitic worms.

Shortly after the middle of the sixteenth century there appeared, in close succession, two great memoirs, both of which contained new observations on worms, evidently made on living specimens. Belon[6]

[1] Pliny, *op. cit.*, Lib. xxxii, cap. xlii, 2; Lib. xi, cap. lii, 1.

[2] *E.g.*, *L. J. Mod. Columella*, De Re Rustica, Lib. vi, cap. xxv; Lib. vii, cap. ix. [Probably written early in the first century.]

[3] Orig. sive Etymolog, Lib. xii, cap. v, p. 106, in Opera Omnia, Emend. J. du Breul, Coloniae Agrippinae (1617).

[4] The words within square brackets are not in the original; they are explanatory comments of the present writer.

[5] De Differentiis Animalium, Paris (1552).

[6] De Aquatilibus, Libri duo, Paris (1553).

(1553) recorded interesting and accurate observations on the earthworm and lugworm, and on their habits. This is the first definite mention of the lugworm, which Belon named *Lumbricus marinus* in contradistinction to the earthworm (*L. terrestris*).

The work of Rondeletius (1554, 1555) surpasses that of any previous writer. Evidently a keen observer, especially of marine animals, Rondeletius described, and gave good woodcuts of, two kinds of *Scolopendrae marinae*, *Hirudo marina*, *Vermis microrynchoteros* and *Vermis macrorynchoteros* [two Sipunculids], *Vermes in tubulis delitescentes* [Serpulids] and *Penicillus marinus* [a Sabellid].[1] In a further paragraph on marine worms[2]—"De vermibus stagni marini"—he gave a short account of "Lumbrici stagni," and in another place[3] referred to *Lumbricus marinus* as being similar to *Lumbricus terrenus*. His figures are, in most cases, faithful representations and were freely copied by Gesner, Aldrovandus and others. Rondeletius added notes on the use in medicine of some of the worms. Gesner's treatise (1558)[4] is, at any rate as regards the articles on worms, a compilation from the works of previous writers, especially Belon and Rondeletius.

Some of the later authors above mentioned, for example, Rondeletius, without proposing any systematic classification of animals, so arranged those which they described as to indicate the possession of some idea of their affinities. One of the earliest classifications in which worms are included is the tabular statement of the subdivisions of "Insects" given by Aldrovandus at the beginning of his treatise "De Animalibus Insectis" (1602). In this Table "Insects" are divided into "Terrestria" and "Aquatica," and each of these is again divided, according to the presence or absence of feet. Among the Terrestria without feet are *Lumbricus terrestris* and worms found in man and animals; among the "Aquatica Pedata" are *Scolopendra marina* and "*Vermes in tubulis delitescentes*" [Serpulids]; in the subdivision "Aquatica apoda" are *Seta aquatica* [*Gordius*], *Hirudo paludosa* and *marina*, *Lumbricus marinus*, *Vermis macrorinchoteros* and *Vermis microrinchoteros* [Sipunculids described by Rondeletius]. Liber VI—"De Vermibus"—of the treatise of Aldrovandus deals with the Terrestria Apoda, including *Lumbricus terrestris* and parasitic worms, but does not

[1] Univ. Aquatil. Hist., pars altera, Lugduni (1555), Liber de Insect. et Zooph., pp. 108–111.
[2] *Op. cit.*, p. 145.
[3] Libri de Piscibus Marinis, Lugduni (1554), p. 399.
[4] Hist. Anim., Liber iiii, Tiguri (1558), pp. 503, 513, 597, 818, 1226, 1227.

refer to any of the marine worms above mentioned; the description of these is given in the following book, which is headed "De Aquaticis." A similar practice was followed by a number of subsequent writers, for instance, Ray and Linnaeus, who placed marine worms among "Insects," and earthworms and parasitic worms in the class "Vermes."

During the next century and a half there appeared several memoirs which included studies and figures of worms. Among these, works by Columna[1] and Bonannus[2] are noteworthy for good figures of a Serpulid and of a Nereid and its jaws; Molyneux[3] gave figures of the external characters and "an account of a not yet described *Scolopendra marina*," evidently an *Aphrodite;* Ellis[4] described and figured tubicolous worms, and Peysonnel[5] published "Observations upon the Sea Scolopendra," in which he described the external features and the action of the pharynx of a nereidiform worm. During this period there were also four works of more outstanding importance by Willis, Redi, Ray and Bonnet. In Willis' classical account[6] of the earthworm the external features, gut, circulatory and reproductive systems are described, and minutiae, such as chaetae, dorsal pores, etc., are discussed. Redi[7] described and figured portions of the anatomy of *Hirudo* and *Lumbricus terrestris,* he noted the occurrence of different species of earthworms, figured *Scolopendra marina* [a nereid] and its alimentary canal, gave descriptions and figures of *Hystrix marina* [*Aphrodite*] and its alimentary canal, and two figures of a Serpulid. Ray in his "Historia Insectorum" (1710) divided "Insects" into those which undergo metamorphosis and those which do not. The latter were subdivided into "Apoda" and "Pedata." Among the "Apoda Terrestria" were placed Lumbrici terrestres (of which Ray distinguished four kinds), and some parasitic worms—"Lumbrici intestinorum"; among the "Apoda Aquatica" were ranged the Hirudines. The "Pedata" were classified according to the number of feet present—six, eight, fourteen or many. Those

[1] Aquat. et Terr. aliquot Anim., pp. xxi, xxii, in Minus Cogn. Stirp., Roma (1616).

[2] Recreatio Mentis et Oculi, in Obs. Anim. Test., Romae (1684), pars i, cap. v, p. 30, tab. ii.

[3] Phil. Trans. R. Soc. Lond., xix (1695), p. 405.

[4] Nat. Hist. of Corallines, London (1755), p. 90, pl. 36, "Tubularia arenosa Anglica" [*Sabellaria*]; p. 92, pl. 34, "Corallina tubularia melitensis" [a Sabellid].

[5] Phil. Trans. R. Soc. Lond., li (1759), p. 35.

[6] De Anima Brutorum, Londini (1672), p. 47.

[7] De Animalculis vivis. Ex Etruscis Latinas fec. P. Costae, Amstelaedami (1708). [1st Edit. 1684.]

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with many feet—the "Polypoda"—were divided into "Terrestria" and "Aquatica"; the section "Terrestria" comprised *Julus* and *Scolopendra*, while the "Aquatica" included "Lugs" and *Scolopendra marina*. This classification of the ametabolous "Insects" followed, in part, that of Aldrovandus; the extensions were due to Ray's friend Francis Willughby. Bonnet[1] instituted an extensive series of experiments and observations on Naids, with special reference to the regeneration following removal of the anterior and posterior ends. A preliminary account of these researches was given in letters to Sir Hans Sloane,[2] in which also remarks were made on similar studies on regeneration in earthworms.

The first edition of Linnaeus' "Systema Naturae" (1735) marks no advance on previous knowledge as regards worms; the only marine worm mentioned therein is *Scolopendra marina*, which is placed in the class Insecta. Among the "Vermes Reptilia" (the class being divided into Reptilia, Testacea and Zoophyta) are *Gordius*, *Taenia*, *Lumbricus* (including *Intestinum terrae*, *L. latus*, *Ascaris*), *Hirudo* and *Limax*. In the sixth edition of the "Systema" (1748) the genera of "Vermes Reptilia" are *Gordius*, *Ascaris*, *Lumbricus*, *Taenia*, *Fasciola*, *Hirudo*, and, included among the "Vermes Zoophyta," are the genera *Amphitrite*, *Nereis*[3] *and Aphrodita*. *Amphitrite* is not mentioned in the tenth or twelfth editions; the reappearance of this name in the thirteenth (Gmelin's) edition is due to the fact that Müller had, in the interval between the twelfth and thirteenth editions, founded a genus of worms with this designation.

In the tenth edition of the Systema (1758), which is now regarded as the foundation of zoological nomenclature, Linnaeus included the genera *Lumbricus* (including the species *terrestris* and *marinus*), *Hirudo*, *Aphrodita*, *Nereis* and *Serpula*, the species of which together number more than forty; in the twelfth edition (1767) *Terebella* and *Sabella* (and *Sipunculus*) were added to the list. The names *Lumbricus* and *Hirudo* had been in use since the time of Pliny, though the former, as defined in the tenth edition, has a much less extensive significance than it bore in pre-Linnaean writings (see p. 2); the other generic names appear to have been used for the first time by Linnaeus.

In the tenth and twelfth editions of the "Systema," Linnaeus divided animals into six classes—Mammalia, Aves, Amphibia, Pisces,

[1] Traité d'Insectologie, 2 Partie, Paris (1745).
[2] Phil. Trans. R. Soc. Lond., xlii (1743), pp. 468–487.
[3] Under which *Scolopendra marina* is given as a synonym.

Insecta and Vermes—distinguished by the number of chambers in the heart and the nature of the blood, the first two classes with "sanguine calido, rubro," the third and fourth "sanguine frigido, rubro" and the last two "sanie frigida, albida." Insects were distinguished by the possession of antennae, Vermes by having "tentacula." It follows from this mode of classification that any invertebrate not having antennae, and therefore not referable to the class Insecta,[1] would fall into the class Vermes, which therefore necessarily became a very heterogeneous assembly. In the twelfth edition (1766–8), which was the last revised by Linnaeus, the class Vermes was subdivided into seven orders—Tardigrada, Imperfecta, Intestina, Mollusca, Testacea, Lithophyta and Zoophyta—only three of which need be considered in this account. The genera were arranged under these three orders in the following manner:—

Vermes Intestina, terrena quondam dicta, ob summam simplicitatem corporis, terebrant omnia. Animalia simplicia, absque artubus, nuda. **Lumbricus,** *Sipunculus*, *Fasciola*, *Gordius*, *Ascaris*, **Hirudo,** *Myxine*.

Vermes Mollusca, nuda, brachiata, vagantur pleraque per maria, ... Animalia simplicia, nuda (absque Testa inhabitata) artubus instructa. *Actinia*, *Ascidia*, *Limax*, *Aplysia*, *Doris*, *Tethis*, *Holothuria*, **Terebella,** *Triton*, *Sepia*, *Clio*, *Lernaea*, *Scyllaea*, **Aphrodita, Nereis,** *Medusa*, *Asterias*, *Echinus*.

Vermes Testacea, mollusca, domiporta, calcareaque domuncula nobilitata .... Animalia Mollusca simplicia, domo, saepius calcarea, propria obtecta. *Chiton*, *Lepas*, *Pholas*, *Mya*, *Solen*, *Tellina*, *Cardium*, *Mactra*, *Donax*, *Venus*, *Spondylus*, *Chama*, *Arca*, *Ostrea*, *Anomia*, *Mytilus*, *Pinna*, *Argonauta*, *Nautilus*, *Conus*, *Cypraea*, *Bulla*, *Voluta*, *Buccinum*, *Strombus*, *Murex*, *Trochus*, *Turbo*, *Helix*, *Nerita*, *Haliotis*, *Patella*, *Dentalium*, **Serpula,** *Teredo*, **Sabella.**

It is evident from this commingling of worms and members of other phyla that the work of previous naturalists and his own observations were not sufficient to indicate clearly to Linnaeus the characteristic features of the worms which we now group together as Annelids, the seven genera of which he placed in three different classes, or even to enable him to separate worms from Mollusca and Echinoderma. Linnaeus had, however, some conception of the affinities of both *Serpula* and *Sabella*, for, after the name of the former genus he added "Animal *Terebella*," and after the name of the genus *Sabella* "Animal *Nereis*" (12th edition, pp. 1264, 1268), and under the species *Sabella alveolata* he stated "Genus hoc multa habet communia cum Nereidibus sed & os & tentacula oris diver-

[1] In both the tenth and twelfth editions of the "Systema" (pp. 639, 1064, respectively), Linnaeus placed *Scolopendra marina* in the class Insecta. In the twelfth edition he stated that this animal was used as bait for herrings. There can be no doubt that one or more species of *Nereis* were thus indicated.

sissima; ....." But the presence of the "test" evidently outweighed these many common characters, so that *Sabella* was not placed near *Nereis* but among the shelled Mollusca.

Gmelin, in his (the thirteenth) edition of the "Systema" (1788), made no advance in regard to the separation of Worms from Mollusca. The only changes from the twelfth edition which call for comment here are—(1) the addition to the Vermes Mollusca of the genera *Amphitrite* Müller, *Spio* Fabricius, and *Nais* Müller; and (2) the removal of the species *Scolopendra marina* from the Insecta, and its reduction to a synonym under *Nereis versicolor* and *noctiluca*. Gmelin seems to have taken practically no notice of the suggestive work of Pallas on *Serpula* (vide infra), for he still retained this worm among the shelled Mollusca placed in the Vermes Testacea, and did not adopt the improved arrangement of some of the worms suggested by Müller (see p. 8).

The stimulus given to the systematic study of animals by the appearance of the "Systema Naturae" soon produced a marked effect on the growth of knowledge in regard to the class of Vermes. Observations on worms, in some cases accompanied by fairly adequate descriptions of their characters, appeared in treatises of natural history, in records of travel and in faunistic works, and there were also accounts or memoirs published on single genera or species. Seba[1] figured *Millepeda marina* [two nereidiform worms], *Eruca seu Scolopendra marina* [*Aphrodite*], *Penicillum marinum* [a Sabellid] and a cluster of slender worm tubes. Baster[2] prepared a series of plates with good figures of the external characters of Nereids, "Scolopendrae plumosae" [Sabellids], Serpulae [including a fragment of a *Lanice* and its tube], "*Hirudo piscium*" [*Pontobdella*], *Aphrodita aculeata*, *A. squamata* [a Polynoid] and *Nereis pelagica*; in the case of the last three some details of the feet were given. Pennant's "British Zoology" (vol. IV, 1777) contains figures of *Lumbricus marinus*, *terrestris* and *minor*, leeches, a Sipunculid, Aphroditidae and Polynoids, Nereids and the tubes of *Serpula* and *Spirorbis*.

Pallas[3] published in 1776 an account of his admirable researches on the anatomy, both external and internal, of *Aphrodita* [including under this name *Aphroditc*, Polynoids and Amphinomids], *Nereis*

[1] Locupl. Rerum Nat. Thes. i, Amstelaedami (1734), tab. lxxxi, 7, 8: tab. xc, 1–3; iii (1758), tab. iv, 7, 8: tab. xvi, 7A, 7B: tab. c. 8.

[2] Op. Subseciva, i, Harlemi (1759–60), tab. iv, v, ix, x; ii (1765), tab. vi.

[3] Miscell. Zool., Hagae Comitium (1766), tab. vii–xi.

cylindraria [*Pectinaria*], *Nereis conchilega* [*Lanice*], *Nereis lutaria* [a Sabellid], *Serpula*, and *Lumbricus echiurus* [*Echiurus*], and in 1788 there appeared a further series of his studies [1] on various "*Nereis*," including "*Nereis lumbricoïdes*" [*Arenicola marina*], and some tubicolous worms [including *Spirorbis*].

Up to the time of Pallas, and, indeed, for a considerable period subsequently, the tubes of *Serpula* were described and figured in works on conchology [2] along with the more loosely coiled gastropod shells; but Pallas showed in his earlier paper [3] that the shell of *Serpula* is different from that of the true Testacea, that *Serpula* agrees fundamentally in structure with *Nereis* and *Aphrodite*, with which it should be united to form an order, in which should also be placed the genera *Lumbricus*, *Hirudo*, *Ascaris*, *Gordius*, and even *Taenia*. Pallas was thus the first to recognise some of the essential differences between worms and molluscs.

Otto Friedrich Müller [4] and Otto Fabricius [5] successfully elaborated the systematic details regarding worms of various kinds, devoting much care to the distinction and definition of genera and species. Müller founded the genera *Amphitrite* and *Nais*, and did much to clarify the diagnoses of previously established genera of worms. His classification of the Vermes (1776)—the class having the limits defined by Linnaeus—is well worthy of notice. He divided the class as follows:—

1. Infusoria [animals living in infusions].
2. Helminthica.
3. Mollusca [similar to the order Mollusca of Linnaeus, except that the genera *Aphrodita* and *Nereis* were transferred to the division Helminthica].
4. Testacea [corresponding to the Testacea of Linnaeus].
5. Cellularia [corresponding to the Lithophyta and Zoophyta of Linnaeus].

The Helminthica found in Denmark and Norway were subdivided into two groups: I. Mutica, containing *Gordius*, *Ascaris*, *Echinorhynchus*, *Hirudo*, *Taenia*; II. Setosa, containing *Lumbricus*, *Nereis*, *Amphitrite*, *Nais*, *Aphrodita*.

This classification marks a distinct advance on that of Linnaeus, showing good progress in the direction of a separation of worms and molluscs. Müller's order Helminthica contains worms only. There

[1] Nova Acta Acad. Sci. Imper. ii, 1784, Petropoli (1788).

[2] See, for instance, d'Argenville's Conchyliologie, Paris, 3 Édit., vi (1780), tab. lxviii.

[3] *Op. cit.* (1766), p. 74.

[4] Vermium Terr. et Fluv., Havniae, i (1773), pars i: pars altera (1774); Zool. Dan. Prodr. (1776).

[5] Fauna Groenlandiæ, Hafniae (1780).

are, however, three worms not included with the rest, namely, *Fasciola* L., the newly defined genus *Planaria* Müller, and *Serpula* L.; but it must be admitted that, taking into account the state of knowledge at that time, these three were difficult genera to place correctly in the scheme of classification. Müller referred *Fasciola* and *Planaria* to the Mollusca, and *Serpula* to the Testacea. He does not appear to have known the work of Pallas on *Serpula;* at any rate, he did not refer to it in his synonymy. Müller was the first to use the presence of chaetae as the distinguishing character of a group of worms.

Blumenbach[1] pointed out that Vermes differ from Insecta not only in the absence of antennae but also of jointed locomotor organs. He was the first to state and emphasise this fundamental difference between the jointed appendages of "Insecta" [*i.e.* Arthropoda] and the feet of worms. His classification closely follows that of Linnaeus.

Barbut,[2] Bruguière[3] and others, produced systematic memoirs based largely on the Linnaean system and reproducing many of its errors. The majority of treatises on natural history published during the last third of the eighteenth century held tenaciously to the Linnaean classification of the Vermes, and in the hands of most workers this class was still in the same unsatisfactory condition as it had been left by Linnaeus. The work of Pallas on *Serpula* and the outline classification given by Müller were the first indications of the dawn of order, which, in the closing years of the eighteenth century, broke upon the chaotic assemblage of Vermes. In 1795 Cuvier communicated to the Société d'Histoire naturelle of Paris a memoir[4] on the circulation in "animaux à sang blanc," in which he described the heart and blood-vessels of various molluscs, and also gave a Table showing the nature of these organs in various classes of animals. The work done in preparation for this memoir brought clearly before him the characters which distinguish worms from molluscs, and from this time forwards Cuvier separated these two classes of animals. In his next memoir—"Tableau élémentaire de l'histoire naturelle des animaux" (Paris, An 6, = 1798)—the two

[1] Handb. der Naturg., Göttingen (1799), 6 Aufl., p. 401. [1st Edit., 1779.]

[2] Genera Vermium, London (1783).

[3] Hist. nat. des Vers in Encyclop. méthod., Paris (1791). Bruguière established a new order in the class Vermes—Vers Échinodermes—to contain the star-fishes, sea-urchins, etc. The other Vermes were left in the same arrangement as in the Systema.

[4] Bull. des Sci. par la Soc. Philom., Paris, i, An iii [1795], p. 91.

classes, Mollusques (p. 372) and Vers (p. 624), are defined and described in some detail, and the "Vers" arranged thus:—

A. Vers pourvus d'épines ou de soies pour s'aider dans leur mouvemens:—

Les Aphrodites.	Les Serpules.	Les Néréides.
Les Amphinomes.	L'Arrosoir.[1]	Les Naiades.
Les Amphitrites.	Les Dentales.	Les Lombrics.
		La Furie.[2]

B. Vers dépourvus d'épines et de soies:—

Les Sangsues.	Les Planaires.	Les Vers intestins.

A comparison of this Table with that of Linnaeus published thirty years previously demonstrates the great advance made in the classification of worms. While much of the credit for this is undoubtedly due to Cuvier, it is also clear that the observations of Pallas and Müller were important contributing factors; it will be observed that *Serpula* is placed near *Aphrodita*, as recommended by Pallas, and that Cuvier, following Müller, used the presence of chaetae as a distinguishing character for one of his subdivisions. The Table presents two defects, namely, the inclusion of Les Dentales [*Dentalium*] and of L'Arrosoir [*Brechites* or *Aspergillum*], but it should be remembered that only the shell of the latter was then known, and that both these are strikingly different in appearance from most Mollusca, the former in particular presenting such a combination of characters that it was not until Lacaze Duthiers (1857) had carefully investigated its anatomy that its systematic position could be safely defined, and then it was found necessary to establish a separate class to receive it.

In his "Leçons d'Anatomie Comparée," published two years later, Cuvier separated worms into two series, according as they possess or lack external organs of respiration.[3] This mode of classification was adopted by Lamarck in his "Système des Animaux sans Vertèbres"

[1] This was first referred to the genus *Serpula* (*S. penis*) by Linnaeus; it was retained in this genus by Cuvier (Règne Animal, p. 522) and others.

[2] A genus established by Linnaeus for a creature named *Furia infernalis* L., said to be found in Eastern Sweden, and described as having a linear, filiform body, provided on each side with a row of pointed hairs. This animal, on coming in contact with mammals or the naked skin of man, was stated to enter the flesh, causing death if treatment were not immediately available. As Bosc remarked (Nouv. Dict. d'Hist. Nat., Paris, An xi [1803], ix, p. 144), it was probably a creature of the imagination, and it is doubtful whether the dried specimen of an animal shown to Linnaeus, by an inhabitant of the country, had any connection with the attacks described. At any rate, *Furia* could not have been a Chaetopod; it may have been a dipterous larva, some of which produce severe myiasis.

[3] See Table at end of Tome i (1805).

(1801). He removed Les Arrosoirs to the Mollusca, but was evidently not certain (p. 98) that this was a correct procedure, and added the new genera *Arenicola* and *Spirorbis*. His arrangement of the worms is tabulated thus:—

1er Ordre. Vers extérieurs (ou externes).

I.—Corps muni d'organes extérieurs.

A. Ceux qui ont des branchies externes . . . . ,
Nereis, Aphrodita, Amphinome, Arenicola, Terebella, Amphitrite, Serpula, Spirorbis, Dentalium.

B. Ceux qui sont dépourvus de branchies externes,
Furia, Nais, Lumbricus, Thalassema.

II.—Corps dépourvu d'organes extérieurs—
Gordius, Hirudo, Planaria.

2me Ordre. Vers intestins—
Fasciola, etc.

Bosc, in his "Histoire Naturelle des Vers" (1802), arranged the genera of worms with external organs (*i.e.* those in Section I. above) in two subdivisions, according as they are nude or live in tubes. In the former division he placed *Aphrodita, Amphinome, Arenicola, Nais, Lumbricus* and *Thalassema*. This was the first time that the presence of a tube had been brought into use as the character of a subdivision.

In 1802 Cuvier[1] stated that he thought it could be shown that all Lombrics, Sangsues, Nayades, Néréides, Aphrodites, Amphitrites and Serpules have red blood, and, though he had not examined the Amphinomes and the rest of the articulate non-intestinal worms, he believed that they would also prove to possess red blood.[2] He gave an account of the vascular system of *Arenicola*, and pointed out, in conclusion, that the possession of red blood by the "Vers articulés" is a very striking character by which they can be distinguished from the intestinal worms.

To this class of segmented worms with red blood, Lamarck, in his course of zoology in 1802, gave the name Annélides,[3] but it was not until some years had passed that the name found general acceptance.

Cuvier, in his "Règne Animal" (1817), divided the Annélides

[1] Bull. Sci. Soc. Philom., Paris, An x [1802], No. 64.

[2] Others remarked that not all Annelids have red blood, *e.g.* Blainville pointed out that in *Aphrodite* the blood is yellow. Nevertheless, the statement of Cuvier may be taken as generally holding good.

[3] Disc. d'ouverture, 27 floréal, An x, Mus. d'Hist. Nat., Paris. "La nouvelle classe des Annélides." See reprint of the discourse in Bull. Sci. Franc. Belg. xl (1907), p. 56.

into three orders[1]—Tubicoles, Dorsibranches and Abranches—using the respiratory organs as the principal distinguishing character. In the Tubicoles the gills are anterior, while in the Dorsibranches they are situated along the sides of the middle part of the body. Cuvier further stated that the genera of the first two orders have bundles of chaetae along their sides, serving as feet; but some genera of the third order do not possess these. He arranged the genera in their orders thus :—

I.—**Les Tubicoles.**	II.—**Les Dorsibranches**	III.—**Les Abranches.**
Les Serpules.	Les Néréides.	Les Lombrics.
Les Sabelles.	Les Eunices.	Les Thalassèmes.
Les Terebelles.	Les Spio.	Les Naides.
Les Amphitrites.	Les Aphrodites.	Les Sangsues.
Les Arrosoirs.	Les Amphinomes.	Les Dragonneaux.[2]
Les Dentales.	Les Arénicoles.	
Les Siliquaires.		

Lamarck[3] (1818) developed the basis of classification. He used additional morphological characters[4] in subdividing the Annelids into three orders, in which he arranged the genera into families, disposed as shown below :—

Apodes.[5]	**Antennées.**[6]	**Sédentaires.**[7]
Les Hirudinées.	Les Aphrodites.	Les Dorsalées (Arénicole, Siliquaire).
Les Echiurées.	Les Néréidées.	Les Maldanies (Clymène, Dentale).
Lombric.	Les Eunices.	Les Amphitrites.
Thalassème.	Les Amphinomes.	Les Serpulées.
Cirratule.		

Savigny[8] adopted practically the same morphological characters[9] as aids to classification, but attached primary importance to the presence or absence of chaetae. He formed four orders by grouping the Annelids around four central genera, which gave their names to

[1] Retained in new edition, iii (1830), and in "Édit. de Disc."
[2] *Gordius*.
[3] Hist. Anim. sans Vert., v, 286.
[4] Probably the introduction of these characters, especially the nature of the chaetae, should be credited to Savigny, who in May 1817 had presented to the Académie des Sciences an account of his researches on the classification of Annelids, and in July of the same year the first part of his classical memoir, which was not published until 1820.
[5] No feet; no feelers; respiratory structures, if any, internal.
[6] Definition as under Nereideae of Savigny (see p. 13).
[7] Definition as under Serpuleae of Savigny (see p. 13).
[8] Syst. des Annél. (1820), p. 5.
[9] See footnote (4) above.

the orders. The orders were thus defined: (1) Nereideae—feet with retractile subulate chaetae but without crotchets, a distinct head with eyes and feelers, and a protrusible proboscis almost always armed with jaws; (2) Serpuleae—feet with retractile subulate chaetae and crotchets, head without eyes or feelers, proboscis not armed with jaws; (3) Lumbricinae—without projecting feet and with chaetae rarely retractile, head without eyes or feelers, and without jaws; (4) Hirudineae—without locomotor chaetae, characterised by the presence of a sucker at each extremity and by having eyes. The families were arranged in the orders thus:—

I. With chaetae for locomotion.
  1. Order Nereideae. Families—Aphroditae, Nereides, Eunicae, Amphinomae.
  2. Order Serpuleae.
    (1) Gills none or few; if present situated on the anterior segments of the body; feet of several kinds.
      Families—Amphitritae, Maldaniae.
    (2) Gills numerous, not on the anterior segments of the body; feet of one kind.
      Family—Telethusae.
  3. Order Lumbricinae. Families—Echiuri, Lumbrici.

II. Without chaetae.
  4. Order Hirudineae. Family—Hirudines.

This is the first list of Annelids published from which all Mollusca are excluded.[1] It is also of interest from our special point of view, as the family Telethusae was formed for the reception of the single genus *Arenicola*.

Savigny's classification is more natural than any of its predecessors, as it is based not on a single feature, but on a group of characters. More than forty years afterwards Prof. Ehlers considered it to be so excellent that he adopted it, with only a slight change, in his monograph on "Die Borstenwürmer," and the classification in use at the present day is based on an extension of the principles of Savigny's system. In addition to his fundamental improvement of the classification of Annelids, Savigny also carefully delimited the known genera and founded more than a score of new ones, most of which remain valid.

Latreille[2] adopted Cuvier's classification in a modified form,

[1] Savigny observed that *Dentalium* was not an Annelid, and he also excluded L'Arrosoir and *Siliquaria*.

[2] Familles nat. Règne Anim., Paris (1825).

the principal change being the formation of an order for the family Téléthuses. His arrangement may be tabulated thus:—

I. Anterior extremity of body usually provided with feelers and tentacles; almost all have feet, and the gills are external.

1. **Notobranches.**	2. **Céphalobranches.**	3. **Mésobranches.**
Aphroditées.	Serpulées.	Téléthuses.
Eunicées.	Sabellées.	
Néréidées.	Amphitritées.	
Solénicoles.[1]	Oecodontes.[2]	
Amphinomées.		

II. No head or antennae, the majority have no feet, organs of respiration internal; live in fresh water or earth, some are parasites.

4. **Entérobranches.**			
Maldanies.	Lombricinés.	Filiformes.[3]	Hirudinées.

This classification shows in a striking manner how a too exclusive use of one character, namely the gills, brings together forms which are really not related. For instance, Latreille placed under the Mésobranches, in the family Téléthuses, the genera *Arenicola* and *Branchellion*, although he remarked that the latter genus appeared to belong to the Hirudinées, but he was so obsessed with the value of the branchiae as a character, that the presence of gill-like outgrowths along the middle region of *Branchellion* outweighed all its other characters. The association of the Maldanies with the earthworms was another mistake of the same kind. The re-introduction of some Mollusca and of *Gordius* among the Annelids was also a retrograde step. Altogether, therefore, the classification of Latreille marked no advance in knowledge, but tended to confusion.

In 1816 Blainville[4] published a classification of the animal kingdom, in which the seventh and eighth classes of articulate animals were designated respectively Sétipodes and Apodes, the former comprising worms with, and the latter worms without chaetae. The class "Apodes" included "Entozoaires" and leeches, which latter were thus separated from the rest of the ringed worms; this class need not be further considered here. The Sétipodes were divided into three orders, according as the rings of the body were markedly dissimilar, slightly dissimilar or similar. In 1828 Blainville[5] re-

[1] For the genus *Spio*.
[2] Contains the genera *Dentalium* and *Siliquaria*.
[3] For the genus *Gordius*.
[4] Bull. Sci. Soc. Philomath., Paris (1816), p. 105.
[5] "Vers," in Dict. Sci. Nat., lvii, Paris (1828). In this later classification the subdivision "Apodes" includes also Sipunculids.

published this classification with a set of new designations for the principal subdivisions, but of all the terms used in his two memoirs only one has survived to the present day; the rest had a very short existence. In his later paper he modified the hybrid term Sétipodes into the more correct Chétopodes. The families were arranged in the order thus:—

Chétopodes.	Hétérocriciens.	Serpulides, Sabulaires.
	Paromocriciens.	Maldanies, Téléthuses.
	Homocriciens.	Amphinomés, Aphrodités, Néréidés, Néréiscolés, Lombricinés, Échiurides.

The chief point of interest in this classification is the clear principle involved in the definite formation and designation of the great division Chétopodes. This division had been foreshadowed by Müller; and Cuvier, Lamarck and Savigny had recognised, to a greater or less degree, the importance of the chaetae as a divisional character, but it was left to Blainville to name the division. The name Chaetopoda has persisted up to the present day, for, in spite of certain disadvantages which it involves, such as the wide separation of earthworms and leeches, it has been found convenient as a descriptive term to designate all those Annelids in which the lateral series of chaetae form a conspicuous feature, by means of which these worms can, with few exceptions, be readily distinguished from all other animals.

The grouping together of the Maldanies and Téléthuses in the order Paromocriciens is noteworthy. Blainville attached less value than most of his contemporaries to the presence or absence of gills as a systematic character, and did not hesitate to associate in one order these two families, although one contains branchiate and the other abranchiate Annelids, because he found them to agree in the nature of their chaetae and in the similar segmentation of the body.

In 1829 Audouin and Edwards presented to the Académie des Sciences their memoir on the classification of Annelids.[1] They stated that they were unable to adopt the classification of either Savigny or Blainville, but the one they presented was, after all, fundamentally that of Savigny and similar to that of Lamarck. The morphological characters used by Savigny were again employed, but in addition the cirri and other soft[2] appendages of the body were taken into account, and thus the limits of the four orders were set forth in

[1] Ann. Sci., Nat., xxvii (1832), p. 337; also in Hist. Nat. Litt. France (1834).

[2] That is, soft in contrast to the chaetae.

greater detail. The Errantes, which are adapted for creeping or swimming, have well developed soft appendages on almost all the body segments. This order, the only one fully considered by the authors, was defined in almost the same terms[1] as the Nereideae (Savigny). The other three orders, named Tubicoles or Sédentaires (with soft appendages aggregated at the anterior end), Terricoles and Suceuses, corresponded nearly[2] to the Serpuleae, Lumbricinae and Hirudines of Savigny. The authors established seven new genera and more than a score of new species. The families of the order Errantes only were given, namely, Aphrodisiens, Amphinomiens, Euniciens, Néréidiens, Ariciens, Péripatiens, Chétoptériens, Arénicoliens.

The orders Errantes and Tubicoles (Sédentaires) of this classification were accepted with little modification by Quatrefages in his "Histoire naturelle des Annelés" and by Claparède in his "Annélides chétopodes du golfe de Naples," and consequently were adopted by nearly all subsequent authors, especially in France and Great Britain, until almost the close of the last century.

The family Téléthuses, founded by Savigny for the genus *Arenicola*, was renamed Arénicoliens by Audouin and Milne Edwards, and this designation, or some modification thereof, recalling that of the genus, has been generally adopted.

The numerous advances in the study and classification of Annelids, made from 1795 until 1834, had been almost entirely due to the labours of the French School, that is, of Cuvier and his disciples, who have left an enduring mark upon this branch of zoology. The stimulus given by their work produced responses in other countries, especially in Britain, Germany and Scandinavia.

Johnston, who drew up a classification of Annelids in 1846,[3] interpreted the limits of the class in a wider sense than Cuvier, Lamarck or Savigny. His classification is fundamentally that of Savigny, with some modification of the limits of the subdivisions, and with the addition of the Nemertina, a decidedly retrograde step.

R. Leuckart[4] (1848) included the Nematodes in the "Annelides" and placed the leeches with the Turbellaria, Trematodes and Nemertines; and Quatrefages[5] (1850) divided the worms into "Vers

[1] Note, however, that *Arenicola* was placed in this order, whereas Savigny included it in the Serpuleae.

[2] As is shown by the families referred to these orders by Edwards in his Élém. de Zool., ii (1834), p. 1016.

[3] Ann. Mag. Nat. Hist., xvi, p. 433.

[4] Morph. u. Verwandtsch. d. wirbell. Thiere (1848), p. 44.

[5] Ann. Sci. Nat. Zool., sér. 3, xiii (1850), p. 7.

dioiques," in which he placed "Annélides," and "Vers monoiques," which included Lombrinés, Hirudinées,[1] Turbellariés and Cestoides. The separation of the earthworms from the rest of the Annelids was unwarrantable and was not followed to any extent by subsequent writers.

Grube's masterly paper[2] on the classification of Annelids appeared in 1850. To him we owe the accurate delimitation of the order Oligochaeta; this he defined so as to exclude such worms as *Cirratulus*, *Trophonia*, *Travisia* and some Gephyrea, which, by previous systematists, had been placed in close association with *Lumbricus*. As a result of his admirable studies on the external features and internal structure of Annelids, and of the critical acumen which he brought to bear on the problem, Grube was enabled to define the limits of this order practically as they stand to-day. He introduced the useful names Polychaeta and Oligochaeta, now universally used and recognised, especially the latter, as designating natural assemblages of worms. Grube's work ranks, with that of Cuvier and Savigny, as one of the great classics on this subject, and was undoubtedly the most important work on the general classification of Annelids published during the seventy years subsequent to the appearance of Savigny's monograph. After giving a detailed account of the structures which he proposed to use in the classification of Annelids, Grube arranged these worms in five orders, which he defined thus:—

I. Appendiculata Polychaeta—Annelids which, besides having lateral bundles of bristles, bear on the dorsum or on the head region either lappets, filaments or compound structures; the bristles are at least eight, and usually many more, in each segment; these animals live in the sea and, as far as is known, are of separate sexes. This order corresponds to the orders Nereideae and Serpuleae of Savigny.

II. Gymnocopa, an order founded to contain the single genus *Tomopteris*.

III. Onychophora for the genus *Peripatus*, which, since the time of Audouin and Edwards, had been considered to be an Annelid.

[1] A considerable number of authors associated the leeches with the flatworms; for instance, van Beneden (1850, 1852-54), Burmeister (1856), Haeckel (1866), Schmarda (1871), O. Schmidt (1872), and Vogt and Yung (1888). But the studies of the development of leeches, especially of their mesoblast (Rathke, 1862), showed that they exhibit the fundamental characters of Annelids, and they were so regarded in the text-books of Gegenbaur, Claus and Huxley.

[2] Arch. f. Naturg., xvi Jahrg., i, p. 249.

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IV. Oligochaeta—Annelids in which the lateral locomotor organs consist of two to eight bristles projecting from scarcely recognisable elevations and not accompanied by cirri, "Lippenblätter" or gills; the genital organs are hermaphrodite, paired, and limited to a few segments; the majority of these worms live in the earth or in fresh water, only a few are found in the sea.

V. Discophora, corresponding to the Hirudineae of earlier systematists.

The Polychaeta were divided into two sub-orders—Rapacia and Limivora—according to the mode of feeding; but, as Grube carefully pointed out, the members of the two sub-orders differ in many of their structural characters. The families of Polychaeta were arranged thus:—

A. Rapacia.		B. Limivora.	
Aphroditea.	Phyllodocea.	Opheliacea.	Maldania.
Amphinomea.	Glycerea.	Pherusea.	Terebellacea.
Eunicea.	Syllidea.	Chaetopterea.	Hermellacea.
Lycoridea.	Amytidea.	Telethusa.	Serpulacea.
Nephthydea.	Ariciea.		

In the years 1865, 1866 there appeared three works on Annelids. In 1865 Johnston's "Catalogue of Non-parasitical worms in the British Museum" was issued, in which these worms were arranged in six orders, as follow:—

A.—Apodous: the body without bristles on the sides.

1. Body exannular.
   - I Order. Turbellaria.[1]
   - II Order. Bdellomorpha.[2]
   - V Order. Gymnocopa.

2. Body annular.
   - III Order. Bdellidea.

B.—Polypodous: the body with bristles along the sides.

- IV Order. Scoloces. Without external soft appendages; the segments with simple spiniform or setaceous bristles, either single or fasciculate.
- VI Order. Annelides. With soft external appendages, and with various bristles collected into fascicles on a more or less protuberant basis.

The Annelides were divided into Rapacia and Limivora, in which tribes the families were arranged as in Grube's classification. The use of the term Annelides for a subdivision which did not include

[1] Included animals now referred to the Turbellaria and Nemertea.
[2] Included the genera *Octobothrium*, *Entobdella*, *Malacobdella*, etc.

such obviously segmented worms as leeches (Bdellidea) and earthworms (Scoloces) was indefensible. The wide separation of *Tomopteris* (Gymnocopa) from its relatives is a further defect of the Table, and there seems no sound reason for the adoption of the term Scoloces for the Oligochaeta of Grube.

Quatrefages (Hist. nat. des Annelés, 1865) also restricted the limits of the class Annélides, excluding from it all worms except the Tubicoles and Dorsibranches (Cuvier) or Errantes (Audouin and Edwards), so that the class, as he defined it, was equivalent to Grube's order Polychaeta plus the Tomopterids. Quatrefages' classification of Annelids depended primarily on the principle laid down by Blainville, namely, the nature of the segments of the worms. Those Annelids in which the segments of the body are similar to each other, and in which, therefore, the body is not divided into distinct regions, were placed in the order Errantes; those in which the repetition of parts is sharply interrupted in one or more places, and in which consequently, the animal is divisible into distinct regions, were placed in the order Sédentaires. These orders were equivalent respectively to the Rapacia and to the Limivora plus Gymnocopa of Grube. The distribution of the families under these two sub-orders is shown below.

Annélides Errantes (A. Erraticae).		**Annélides Sédentaires (A. Sedentariae).**	
Aphroditiens.	Chlorèmiens.	Chétoptériens.	Leucodoriens.
Palmyriens.	Néréidiens.	Tomoptéridiens.	Hermelliens.
Euniciens.	Syllidiens.	Clymèniens.	Pectinairiens.
Lombrinériens.	Hésioniens.	Arénicoliens.	Térébelliens.
Amphinomiens.	Phyllodociens.	Ophéliens.	Serpuliens.
Nephtydiens.	Glycèriens.	Ariciens.	
Nériniens.	Polyophthalmiens.		
Cirrhatuliens.			

Prof. Ehlers[1] admitted that the order Oligochaeta, as defined by Grube, formed a natural assemblage, but was doubtful whether the order Polychaeta could be so regarded. He preferred the system of Savigny, which he praised as embodying the soundest principles. He regarded the three sub-orders Nereideae, Serpuleae and Lumbricinae (the latter, of course, exclusive of the Echiuroidea) as representing three essentially different types of Chaetopoda; but finding that certain genera could not be properly placed in these orders, Prof. Ehlers founded a fourth sub-order, Ariciea, intended to contain genera which had been placed by some authors in the Nereideae and by others in the Serpuleae. Only the sub-order Nereidea was con-

[1] Die Borstenwürmer, Leipzig (1866), pp. 52–57.

sidered; no doubt the genus *Arenicola* would have been described under the Ariciea had the work on these lines been continued.

The classification of the Polychaeta followed by most writers from 1865 onwards was that of Audouin and Edwards and of Quatrefages, that is, the order was subdivided into Errantia and Sedentaria. A considerable number of writers, no doubt finding difficulty in deciding whether certain families or genera[1] should be referred to the Errantia or to the Sedentaria, discarded these sub-orders, and, like Malmgren, for instance, adopted the plan of placing the families in such sequence as seemed to them to indicate best their relationships to each other.

Dr. Levinsen[2] ranged the "Annulata" in three main divisions —Chaetopoda, Gymnocopa (for *Tomopteris*) and Discophora (Leeches). The Chaetopoda were divided into Polychaeta and Oligochaeta. Dr. Levinsen grouped the families of Polychaeta so as to form eleven sub-orders, which, however, he did not define. These sub-orders and their families were arranged thus :—

Phyllodociformia.

(1) *P. vera.*
Phyllodocidae.
Alciopidae.

(2) Nephthydae.

Aphroditiformia.

(1) *A. vera.*
Aphroditidae.
Polynoidae.
Acoëtidae.
Sigalionidae.

(2) Palmyridae.

Sternaspiformia.

Sternaspidae.

Amphinomiformia.

(1) *A. vera.*
Amphinomidae.
Euphrosynidae.

(2) *A. arenicolina.*
Telethusae.
Scalibregmidae.

Euniciformia.

(1) *E. vera.*
Eunicidae.
Onuphidae.
Lumbrinereidae.
Staurocephalidae.

(2) *E. glycerina.*
Goniadidae.
Glyceridae.

Syllidiformia.

(1) *S. vera.*
Nereidae.
Hesionidae.
Syllidae.
Nerillidae.
Sphaerodoridae.

(2) *S. spionina.*
Spionidae.
Chaetopteridae.
Cirratulidae.
Ariciidae.
Chloraemidae (?).
Ophelidae (?).

Terebelliformia.

Terebellidae.
Ampharetidae.
Amphictenidae.

Maldaniformia.

Maldanidae.
Capitellidae.

Ammochariformia.

Ammocharidae.

Hermelliformia.

Hermellidae.

Sabelliformia.

Sabellidae.
Serpulidae.

[1] *Arenicola*, for instance, was placed by some authors in the Errantia, by others among the Sedentaria. The Ariciidae presented a similar difficulty.

[2] "Syst.-geog. Overs. nordiske Annulata," etc., in Vid. Medd. naturh. Foren. Kjøbenhavn 1882 (1883), p. 180.

This classification is an extension of Savigny's method—*i.e.* the families are grouped around a central type; they are classified not by definition but by type, not by precept but by example. Although this arrangement presents certain advantages over any previous classification, it does not by any means solve the difficulties which arise when the attempt is made to group the families of Polychaeta; see, for instance, the assemblage of divergent forms brought together under the group Syllidiformia spionina. The close relationship of the Arenicolidae and Scalibregmidae is well represented in this classification, but the association of these families with the Amphinomidae does not appear to be justified by any community of structure.

During the ten years following the publication of Dr. Levinsen's memoir no marked changes were introduced into the mode of classification of Polychaeta; most writers during this period adopted the subdivisions Errantia and Sedentaria, others considered the families separately in such order as each author thought best.

In 1893 Prof. Hatschek and in 1894 (and 1896) Prof. Benham suggested new classifications of the Polychaeta. Prof. Benham's classification,[1] which combines, to some extent, the systems of Quatrefages and Levinsen, divides the Polychaeta into two grades or branches—(a) the Eucephala, later[2] named Phanerocephala, in which the prostomium retains its original condition as a lobe overhanging the mouth and is not overgrown by the peristomium; the body-segments are similar so that the body is not divided into regions; (b) the Cryptocephala, in which the peristomium grows forwards and fuses with or entirely conceals the greatly reduced prostomium; the body-segments are differentiated into two regions by a sudden change in the character and arrangement of the chaetae, and also by certain internal differences. The arrangement (1896) of the families in the sub-orders is shown in the following Table:—

A. PHANEROCEPHALA.

Nereidiformia.

Syllidae.
Hesionidae.
Aphroditidae.
Phyllodocidae.
Tomopteridae.
Nereidae.
Nephthydidae.
Amphinomidae.
Eunicidae.
Glyceridae.
Sphaerodoridae.
Ariciidae.
Typhloscolecidae.

[1] Rep. Brit. Assoc. (1894), p. 696.
[2] Cambr. Nat. Hist., vol. ii (1896), p. 258.

A. **PHANEROCEPHALA** (*continued*).

Spioniformia.
Spionidae.
Polydoridae.
Chaetopteridae.
Magelonidae.
Ammocharidae.

Terebelliformia.
Cirratulidae.
Terebellidae.
Ampharetidae.
Amphictenidae.

Capitelliformia.
Capitellidae.

Scoleciformia.
Opheliidae.
Maldanidae.
Arenicolidae.
Scalibregmidae.
Chlorhaemidae.
Sternaspidae.

B. **CRYPTOCEPHALA.**

Sabelliformia.
Sabellidae.
Eriographidae.
Amphicorinidae.
Serpulidae.

Hermelliformia.
Hermellidae.

Although this classification has many good points it is not without defects; for instance, the great sub-order Nereidiformia, which contains about half the number of families and of genera of Polychaeta, is rather unwieldly, and not entirely homogeneous. The families Maldanidae, Arenicolidae and Scalibregmidae, and possibly the Opheliidae, contain series of more or less closely related worms; associated with these, in the sub-order Scoleciformia, are the Chlorhaemidae and Sternaspidae, which stand considerably apart from the preceding quartette; but if the two latter families are not included in the Scoleciformia they cannot be referred to any other sub-order, and the formation of one or two new sub-orders would be required for their reception.

In Prof. Hatschek's classification[1] the Polychaeta are separated into two main subdivisions—namely, the Cirrifera—those in which parapodial cirri are present, and in which the homonomy of the segments is little disturbed—and Acirra—which are without clearly marked parapodial cirri and in which heteronomy of the external and internal structures indicates a division into regions. This classification may be tabulated thus—

A.—**CIRRIFERA.**

1. **Spiomorpha.**

Spionidae.
Ariciidae.

Appendices: Chaetopteridae.
Pherusidae.
Opheliidae.

[1] Lotos, xiii (1893), p. 123.

2. **Amphinomorpha.**
   Amphinomidae.

3. **Rapacia (Nereimorpha).**
   Glyceridae.
   Nephthydidae.
   Eunicidae.
   Aphroditidae.
   Stephanidae.
   Nereidae.
   Hesionidae.
   Syllidae.
   Phyllodocidae.
   Sub-fam. Phyllodocinae.
   Alciopinae.
   Hydrophaninae.
   Tomopterinae.
   Appendix: Myzostomidae.

B.—**ACIRRA.**

4. **Drilomorpha.**
   Cirratulidae.
   Arenicolidae.
   Capitellidae.
   Maldanidae (incl. Ammocharidae).
   Appendices: Sternaspidae.
   Ctenodrilidae.

5. **Terebellomorpha.**
   Amphictenidae.
   Terebellidae.

6. **Serpulimorpha.**
   Hermellidae.
   Serpulidae.

The above arrangement, with a few slight alterations, was adopted by Profs. Claus and Grobben,[1] who, however, did not employ the division into Cirrifera and Acirra, a change for which there is full justification. They divided the Polychaeta directly into six sub-orders, similar in constitution to those defined by Prof. Hatschek, except that the Opheliidae were removed from the Spiomorpha to the Drilomorpha. This classification presents defects, similar to those associated with Prof. Benham's arrangement, in regard to the great size of the sub-order Rapacia and the heterogeneous contents of the sub-order Drilomorpha. Further, there seems to be little warrant for the inclusion of the Pherusidae (Chlorhaemidae) in the sub-order Spiomorpha.

Summary.—The systems of classification of the Polychaeta, which have been suggested and have met with acceptance during the last hundred years, may now be summarised and the position of the family Arenicolidae (or Telethusae) indicated in each.

I. Cuvier (1817) distinguished two orders of marine worms—Les Tubicoles and Les Dorsibranches—by the position of the gills, which in the former are massed at the anterior end, while in the latter they are distributed along the body, as, for instance, in *Arenicola*. This

[1] Lehrb. d. Zool., Marburg (1905).

principle of classification was maintained, especially during the twenty years subsequent to its enunciation, by a number of writers who placed the family Telethusae in an order designated Dorsibranches, Notobranchia or Mésobranches.

II. Savigny (1820) divided marine worms, according to the characters of the chaetae, head and proboscis, into two orders—Nercideae and Serpuleae, to the latter of which the family Telethusae was referred. The principles of classification laid down by Savigny were adopted and extended by later workers, few of whom, however retained the original ordinal names.

III. Orders of similar constitution to those of Savigny were proposed by Lamarck (1818) and named Antennées and Sédentaires, and by Audouin and Edwards (1832), who separated the Errantes from the Sédentaires by their mode of life. This classification was adopted by Quatrefages (1865), and the ordinal names Errantia and Sedentaria were in general use during the next thirty years. Audouin and Edwards placed *Arenicola* in the order Errantes, but Lamarck, Quatrefages and most other writers have referred it to the Sedentaria.

IV. Grube (1850) used the mode of feeding, and certain morphological characters, as a means of separating the Polychaeta into two sub-orders—Rapacia and Limivora, to the latter of which *Arenicola* was referred. This system of classification was adopted by Johnston (1865) and others.

V. The systems of Profs. Benham and Hatschek are based on anatomical characters, and divide the Polychaeta into six or seven sub-orders. The family Arenicolidae is placed in the sub-order Scoleciformia (Benham), which is similar to the sub-order Drilomorpha (Hatschek), the chief features of which may be stated thus—the prostomium[1] seldom bears sensory processes, the peristomium[2] has no cirri, the parapodia[3] are feebly developed and may be absent, cirri[4] are usually wanting, true uncini[5] are not present, the buccal region and pharynx are eversible and there are no jaws, some or many of the septa are wanting, and the nephridia are reduced to a comparatively few pairs, which are all alike.

[1] The anterior portion of the head, namely, that part which is pre-oral; equivalent to the "head-lobe," or "Kopflappen" (Grube) of some earlier writers.

The posterior portion of the head, immediately following the prostomium, and bearing the mouth.

[3] Paired, unjointed, lateral outgrowths of the body wall in each body-segment, bearing chaetae and serving as organs of locomotion.

[4] Filamentous sensory processes.

[5] Chaetae in the form of short and sharply curved hooks, characteristic especially of Terebelliformia and Sabelliformia.

It is evident from the preceding pages that the Polychaeta form is an order difficult to classify, and it must be admitted that none of the classifications hitherto proposed surmounts the many difficulties involved. It will therefore be preferable, in the present state of the subject, to adopt the method of most recent workers on Polychaeta, that is, to consider the families separately, and in such order as convenience directs. The families placed in the sub-order Scoleciformia seem especially to call for reconsideration; but, until further information is available with regard to some of them, particularly the Chlorhaemidae and Opheliidae, nothing definite in the way of a change of the constitution of the sub-order can be made. The present Catalogue will place the knowledge of one of the families on a broader basis and provide material which may be used in discussing the affinities of this with other families of the sub-order.

ARENICOLIDAE Johnston, 1835.

Telethusae—
Savigny, Syst. Annél. (1820), p. 95.
Johnston, Catal. Worms Brit. Mus. (1865), p. 226.
Levinsen, Vid. Medd. Naturh. Foren. Kjöbenhavn (1883), p. 133.

Telethusae, *partim*—
Latreille, Fam. nat. Règne Anim. (1825), p. 244.

Telethusa, *partim*—
Danielssen, K. Norske Vid. Selsk. Skr., iv (1859), p. 121.
Grube, Arch. Naturg., xvi Jahrg., i (1850), p. 322.
Schmarda, Neue wirbell. Thiere, i, 2 Hälf. (1861), p. 51.

Thelethusidae—
Cunningham and Ramage, Trans. R. Soc. Edin., xxxiii (1888), p. 648.

Arenicolidae—
Johnston, Loudon's Mag. Nat. Hist. viii (1835), p. 566; Ann. Mag. Nat. Hist., xvi (1845), p. 454.
Ashworth, Liverpool Mar. Biol. Comm., Mem. xi (1904), p. 71.
Fuchs, Jenaische Zeits., xlii (1907), p. 388.
Gamble and Ashworth, Q. J. Micr. Sci., xliii (1900), p. 538.
Lo Bianco, Atti R. Accad. Sci. Fis. Mat. Napoli, v, ser. 2, no. xi (1893), p. 9.

Arenicolidae, *partim*—
Johnston, Ann. Mag. Nat. Hist., iv (1840), p. 373.

Arénicoliens—
Audouin et Edwards, Ann. Sci. Nat., xxx (1833), p. 418; Hist. nat. Litt. France, ii (1834), p. 282.
Fauvel, Mém. Soc. Nation. Sci. Nat. Math. Cherbourg, xxxi (1899), p. 161.
Mesnil, Bull. Sci. France Belg., xxx (1897), p. 145.
Quatrefages, Hist. nat. Annel., ii (1865), p. 259.

Arénicoliens, *partim*—
Edwards, in Lamarck's Hist. nat. Anim. s. Vert., 2e Edit., v (1838), p. 513.

Polychaeta of elongate, cylindrical form, which, when adult, bear gills on a number of successive chaetiferous segments; prostomium without tentacles or palps; peristomium without cirri, followed by an achaetous segment and by a number of chaetiferous segments, each of which bears dorso-laterally a tuft of capillary chaetae, and, more ventrally, a row of crotchets; an achaetous "tail" is present in some species. The pharynx has no jaws, but bears series of papillae, the tips of which, in large specimens, may be capped with chitin; glandular caeca, one or more pairs, are present on the posterior part of the oesophagus; coelomic septa have disappeared in the region of the body in which the "stomach" is situated, but septa are constantly present at the anterior border of the first, third and fourth chaetiferous segments, and also in a greater or less extent of the intestinal region. Nerve-cord non-ganglionated.

Type Genus.—*Arenicola* Lamarck.

Historical Account.—The family Telethusae[1] was founded by Savigny for the genus *Arenicola,* only one species of which, *A. marina* (then usually designated *A. piscatorum* Lamarck) was known.

Latreille included *Branchellion*—a genus of leeches—in this family, for the sole reason that, like *A. marina,* it possesses gills on the middle segments of the body.

In 1833 Audouin and Edwards designated the family, in which they placed only the genus *Arenicola,* Arénicoliens, and two years later the latinised form Arenicolidae was first used in an article by Johnston. These names have been adopted by most subsequent writers in preference to the original family name. It is a little remarkable that Johnston, after using the name Arenicolidae in his papers in 1835, 1840 and 1845, reverted in his British Museum Catalogue[2] to the use of the designation Telethusae.

Several authors have attempted to add other genera to the family, or to use the family name in an extended sense; but, with one exception, these changes have not been attended with success. The term Arénicoliens was used by Edwards in 1838,

[1] Telethusa, the wife of Lygdus and mother of Iphis. *Ovid,* Metam., ix, 682.

[2] The name Arenicolidae is given (p. 214) as if it were a synonym of the sub-order Limivora.

to designate a division in which he placed two tribes, namely, Arénicolides, including the genera *Arenicola* and *Chaetopterus*, and Ariciens, comprising the genera *Cirratulus, Ophelia, Aricia* and *Aonis*. This usage of the name Arénicoliens was inconvenient, since the six genera referred to the family formed an obviously heterogeneous assemblage; the conjunction of *Arenicola* and *Chaetopterus* was especially indefensible, and was not accepted by subsequent authors. In 1840 Johnston placed the new genus *Travisia* in the family Arenicolidae, but he soon reached the conclusion that it was desirable to remove it, for in his "Index to the British Annelides," published in 1845, *Travisia* is found under the family Lumbricidae.

Grube was led by the general external resemblance between *Arenicola* and his new genus *Dasybranchus* to add the latter to the family Telethusa; Danielssen referred three genera to this family, namely, *Arenicola, Scalibregma* Rathke and *Notomastus* Sars. Schmarda carried the inclusive process still further, placing in the family the genera *Arenicola, Dasybranchus, Eumenia* Örsted and *Scalibregma*. But Grube and Malmgren successively curtailed the family by removing genera. Grube[1] created a new family—Capitellacea—for the reception of *Dasybranchus, Notomastus* and the allied genus *Capitella* Blainville, and Malmgren founded the family Scalibregmidae for the genera *Eumenia* and *Scalibregma*, and thus reduced the family Thelethusae[2] to the single genus *Arenicola*.

A second genus was added to the family in 1881 when Langerhans defined his newly discovered *Branchiomaldane vincenti* as a Telethusan with simple filamentous gills.

Prof. Mesnil (1897) gave an account of *B. vincenti*, and of three species of *Clymenides—sulfureus, ccaudatus* and *incertus*[3]—and pointed out the resemblances of these small Polychaetes to *Arenicola* on the one hand and to the Maldanidae on the other. Regarding them as connecting links between the families Arenicolidae and Maldanidae, he proposed to indicate the continuous series of forms presented by these two families by combining them into one family, the "Arénicolo-Maldaniens," which, however, he regarded as divisible into two tribes, Arénicoliens and Maldaniens, differentiated by the nature of their segments, "courts et assex nombreux" in Arénicoliens, "longs et peu nombreux" in Maldaniens. Although the relationship

[1] Arch. Naturg., xxviii Jahrg., i (1862), p. 366.
[2] Öfvers. K. Vet. Akad. Förh., 1867 (1868), p. 188.
[3] Since proved to be post-larval stages of *Arenicola marina, ccaudata* and *B. vincenti* respectively.

between the Arenicolidae and Maldanidae is obvious and admitted, it is not sufficiently close to justify the fusion suggested by Prof. Mesnil. Moreover, the affinities of the Arenicolidae are not entirely with the Maldanidae, but also with the Scalibregmidae. The degree of relationship in which these families stand to each other cannot be determined fully until further investigations have been carried out, but it seems to the present writer highly improbable that the results of such investigations will lead to the fusion of any two of them. These three families present characters which appear to indicate their evolution along independent lines; a discussion of their affinities will be found on pp. 160, 161.

The account of *Branchiomaldane* (p. 147) shows that this genus presents several resemblances to *Arenicola*, and that it must be included in the family Arenicolidae, but the writer is not prepared to follow Prof. Fauvel in merging the two genera, as they present important differences, especially in regard to the gills, nephridia, gonads and early stages of development.

The family Arenicolidae is therefore regarded as containing two genera, adult examples of which may be distinguished by the characters given in the following key:—

Branchial segments subdivided into five annuli; gills much branched, borne on the chaetiferous annulus; prostomium small and may be sunk in the deep nuchal invagination; dioecious, gonads borne on the nephridia only; an achaetous tail in some species.... ..... *Arenicola*, p. 29.

Branchial segments for the most part subdivided into two rings, one chaetiferous, the other branchiferous; gills composed of one to four finger-shaped filaments; prostomium large, nuchal groove shallow; monoecious, gonads borne on the septa and oblique muscles; ecaudate; small, not more than 2 cm. long..... *Branchiomaldane*, p. 147.

Young post-larval stages of the ecaudate species of *Arenicola* exhibit a general external resemblance to *Branchiomaldane*, but the presence in the latter of gonads, and of bi-annulate branchial segments in which the chaetae and gills are borne on consecutive annuli, and the absence of statocysts and pigment, are useful differential characters.

ARENICOLA Lamarck, 1801, emend.

Arenicola—
Lamarck, Syst. Anim. s. Vert. (1801), p. 324; Hist. Anim. s. Vert., v (1818), p. 335.
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Arenicola, *partim*—
Fauvel, Mém. Soc. Nation. Sci. Nat. Math. Cherbourg, xxxi (1899), p. 161.

Chorizobranchus—
Quatrefages, *op. cit.*, p. 267.

Clymenides—
Claparède, Beobacht. Anat. wirbell. Thiere Normand. (1863), p. 30.

Clymenides, *partim*—
Mesnil, Bull. Sci. France Belg., xxx (1897), p. 148.

Lumbricus, *partim*—
Linnaeus, Syst. Nat., x Edit., i (1758), p. 647: xii Edit., i, 2 (1767), p. 1076.

ADULT.—Arenicolidae usually found burrowing in sand; pairs of branched gills are borne dorsally on the chaetiferous annuli of a number of the segments, in the caudate species on all except the first six, and in the ecaudate species from the twelfth or sixteenth usually to the last. Prostomium small, bounded posteriorly by the nuchal invagination. Each chaetiferous segment, except the first three or four, is subdivided usually into five annuli, that which bears the parapodia being larger than the others. Each parapodium consists of a conical notopodium bearing capillary chaetae, and a neuropodium in the form of a muscular ridge, traversed by a deep groove, in which a row of crotchets is situated. In some species there is a posterior "tail," composed of achaetous segments. There is a pair of hearts a short distance behind the oesophageal glands. The first nephridium opens on the fourth or fifth segment, the dorsal lip of

the funnel is fringed with ciliated vascular processes, the margin of the ventral lip, which is not fringed, is either entire, frilled, or deeply notched in the middle. Dioecious, the reproductive organs are borne on the nephridia only. There is a pair of statocysts in the peristomium (except in *A. pusilla*).

Post-larval Stages.—Arenicolidae found either pelagic, or semi-tubicolous, living among algae or in sand. Gills absent, or present on a few segments, but small. Prostomium large, conical and overhanging the mouth; nuchal groove present. Annulation either absent or as in adult. Capillary chaetae and crotchets present in each chaetiferous segment, a transient crotchet in some of the later formed notopodia. An achaetous "tail" in some species. Hearts and nephridia present, the latter have either larval funnels or simple early phases of the adult funnel. Reproductive organs absent or minute. A pair of statocysts in the peristomium (except in *A. pusilla*).

Type Species.—*A. marina* (Linnaeus).

Historical Account.—The first mention of a representative of this genus is found in Belon's De Aquatilibus (1553), in which observations are given on the common lugworm, to which Belon gave the name *Lumbricus marinus*. *L. marinus* is not mentioned in the first edition of the Systema Naturae, but Linnaeus recorded and figured it in the account (1747) of his journey through West Gothland, and placed it in the sixth and subsequent editions of his Systema. The descriptions of the lugworm given by Pallas, Fabricius and others before the end of the eighteenth century served to bring into notice differences between this worm and the earthworm, which led Lamarck, in 1801, to place these two worms in separate genera.[1]

[1] Gervais (*op. cit.*) states that Boucher d'Abbeville first indicated, in 1798, that the lugworm should be placed in a genus apart from *Lumbricus*. The writer has searched carefully for publications by Boucher in the hope of finding his remarks on this point, and is indebted for help to M. Ch. Gravier, who has also spent considerable time in the same quest, among the literature of the period, in the Library of the Muséum d'Histoire Naturelle, Paris. Only one paper by Boucher, dealing with *Lumbricus marinus*, can be found (Soc. d'Émulation d'Abbeville, Cl. Sci. et Arts, Rapp. du Trimestre de Vendémiaire, An 7), but this does not contain any indication of a division of the genus *Lumbricus*. Fortunately, there is not even a suggestion that Boucher put forward a name for the alleged new genus, so that there is no danger of the generic name *Arenicola* losing priority and falling, as so many other well-known names have done of late, into the limbo of synonymy.

The earthworm was left in the old genus *Lumbricus*, and the lugworm removed to a new genus *Arenicola*,[1] because, as Lamarck observed in 1818, the presence of external gills rendered impossible its retention in the genus *Lumbricus*. Lamarck then (1818) gave a fuller diagnosis of the genus *Arenicola*, based on the single species (*A. piscatorum* = *marina*) known to him, in the following terms: "Corpus molle, longum, annulatum, cylindricum, postice nudum; setarum fasciculi biseriales in parte media anticaque. Branchiarum externarum arbusculae aut penicilli ad basim fasciculorum dorsalium. Os terminale nudum. Oculi nulli."

Audouin and Edwards (1833) described, from specimens which were doubtless ecaudate, a species, *A. branchialis*, which differs from the lugworm in the number and arrangement of its gills, and in 1835 Johnston described the species *A. ecaudata*. The discovery of this species, in which the feet and gills extend to the posterior end of the worm, necessitated an emendation of Lamarck's diagnosis of the genus, the statement "postice nudum" being no longer applicable to the genus as a whole. But a considerable number of writers, including Johnston (1865), continued to define the genus *Arenicola* by stating the characters of the lugworm only, neglecting completely the existence of the ecaudate species.

Suggestions for a subdivision of the genus have been put forward by Lütken and Prof. Mesnil. Lütken[2] proposed that *A. antillensis* (= *cristata*) should be placed in a sub-genus *Pteroscolex*, because of the feathered or pinnate nature of the gills. He made this proposal evidently with some diffidence, for he remarked that, in regard to its other external features, this worm was a typical "Sandorm." Claparède (1868) promptly rejected this sub-genus on the ground that a similar form of gill to that occurring in "*Pteroscolex*" had been found by Williams in examples of the common lugworm.[3]

Prof. Mesnil[4] proposed to retain in the genus *Arenicola* those species with a small number of segments—seventeen to nineteen—and a long achaetous tail, namely, *A. marina*, *claparedii* (= *pusilla*) and *cristata*, but to erect a new genus *Arenicolides* for the two species —*branchialis* and *ecaudata*—having a large number of chaetiferous segments and no tail. The writer, while not prepared to go so far as Prof. Mesnil suggests, admits that there is something to be said in

[1] *Arena*, sand; *colere*, to inhabit.
[2] Vid. Medd. Naturh. Foren. Kjöbenhavn, 1864 (1865), p. 121.
[3] The gills of some specimens of *A. marina* are almost as highly pinnate as those of *A. cristata*.
[4] Bull. Sci. France Belg., xxxii (1899), p. 326.

favour of the recognition of the differences between the caudate and ecaudate species. The latter differ from the former in their brain and prostomium, in the absence of tail, and in the mode of branching of their gills, but the two ecaudate species diverge very sharply from each other in the number of their nephridia and the nature of their reproductive organs; in regard to the last-named character especially the differences between *A. branchialis* and *A. ecaudata* are as great as between the latter and any caudate species. The opinion of the writer is that the caudate and ecaudate species present such a number of common characters as to warrant their inclusion in a single genus, and that the differences presented by the ecaudate species would be sufficiently recognised by regarding them as of sub-generic importance. It is therefore proposed to maintain all the species in the genus *Arenicola*.

Prof. Fauvel has merged *Branchiomaldane* with *Arenicola*, but, for reasons set forth in another part of this volume (p. 155), the writer does not consider this advisable, and therefore maintains the two genera.

Quatrefages' genus *Chorizobranchus* was based on his interpretation of a badly executed figure of "*Lumbricus marinus*," given by Delle Chiaje in 1825, in which the branchiferous segments are shown separated by abranchiate ones. There can be no doubt that this figure was intended by Delle Chiaje to represent a specimen of *Arenicola*, for in 1841 he himself cited the figure among the synonyms of *A. piscatorum*. This new genus, being established on an obviously defective basis, as Claparède soon pointed out, was not recognised by any subsequent writer.

The genus *Clymenides* (see p. 75), as defined in the single species *sulphurea* of its author, Claparède, is merged with *Arenicola* because the worm described under this name was almost certainly a post-larval stage of *A. marina*. The examples of *C. sulfurcus* described by Prof. Mesnil were undoubtedly young stages of *A. marina*, and his two new species *C. ecaudatus* and *incertus* have been proved to be young phases of *A. ecaudata* and *Branchiomaldane vincenti* respectively.

A GENERAL ACCOUNT OF THE GENUS *ARENICOLA*.

The following account of the genus *Arenicola* relates to the external features, and to those internal organs which are used as factors in diagnosis in the subsequent part of this Catalogue.

External Characters.—All the species of *Arenicola* are elongate, cylindrical worms, which live, when adult, in sand or mud, or in coarse gravel. Some of the species, especially *A. marina, loveni* and *cristata*, may attain a length of 400 mm.; one specimen of *A. cristata* was as much as 515 mm. long and 75 mm. in girth.

Examples of this genus have the morphological components found in other Polychaeta, namely, prostomium, peristomium, a number of body-segments, and a terminal segment or pygidium, but the last named has generally been lost in the adult. A certain number, or all, of the body-segments (except the first) bear parapodia, but the latter and the prostomium are considerably modified and reduced, as compared with the corresponding structures of more active, mobile Polychaeta, such as *Nereis* (Pl. XII, Figs. 36, 37, 38).

In the caudate species of *Arenicola* the prostomium (Figs. 1, 2) is a small trilobate structure,[1] which, even in large specimens, seldom

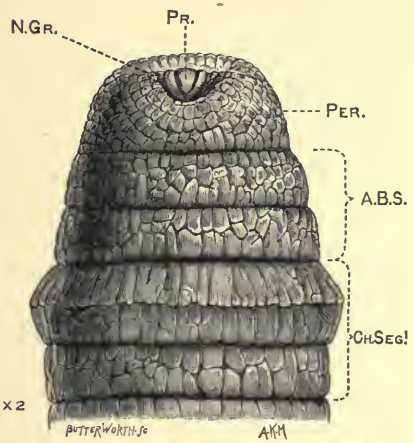

Fig. 1.—*Arenicola loveni.* Anterior end, dorsal aspect. PR. Prostomium; PER. Peristomium; N.GR. Nuchal groove; A.B.S. Achaetous body-segment; CH.SEG.[1] First chaetiferous segment.

Fig. 2.—*A. pusilla.* Anterior end, dorsal aspect; showing the large and folded lateral lobes of the prostomium.

exceeds 2 mm. in diameter, and, since it is liable to be retracted within the crescentic nuchal groove situated immediately behind it, is often seen with difficulty, and then only in part. The prostomium

[1] Fabricius (Fauna Groenl. (1780), p. 284), in describing *Lumbricus papillosus* (=*A. marina*), mentioned the presence of a short, foliate, trifid "rostrum," and Savigny drew attention to this small, trilobed "caroncule," but its nature was not understood thoroughly until Dr. Levinsen (1883) pointed out its homology with the head-lobe (prostomium) of *Scalibregma.*

does not bear any sensory processes—tentacles or palps—and though eyes are present they are minute and sub-epidermal, and are not visible on external examination, except in the case of specimens less than 10 mm. in length.

The proportionate size of the median and lateral lobes of the prostomium varies considerably in the different caudate species, and forms a useful specific character—for instance, in *A. loveni* the median lobe is large, while in *A. pusilla* the lateral lobes are very highly developed (*cf.* Figs. 1, 2). In the two ecaudate species the prostomium forms a transverse ridge, the mid-dorsal portion of which, in some specimens, is slightly elevated above the rest (Fig. 3). In these species the prostomium merges anteriorly with the dorsal oral papillae, which form an "upper lip," while posteriorly it is bounded by the nuchal groove. The conical anterior end of each of these species is therefore not entirely prostomial in nature, it is constituted also, in fact largely, of the "upper lip." *A. pusilla* possesses the most complex and highly developed prostomium, while the two ecaudate species stand, in this respect, at the opposite end of the series, the prostomium being feebly developed. The prostomium is large in the larval and post-larval stages (see Pl. X), and in these its pre-oral nature is well seen. In the adults of all species, however, the prostomium is much smaller, relatively to the peristomium and following segments, than in larval and post-larval stages, and is not pre-oral in position, for it is situated behind the "upper lip."

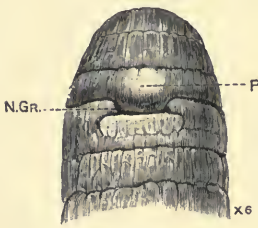

Fig. 3.—*A. branchialis.* Anterior end, dorsal aspect. N.GR. Nuchal groove; PR. Prostomium.

In *Arenicola* the segmentation of the body is somewhat obscured by the subdivision of each segment into rings or annuli. The annuli are generally five in number, and one, larger than the rest, bears the parapodia.

The parapodia are obviously much reduced, as compared with those of *Nereis* (Pl. XII, Fig. 38), no doubt in correlation with the very different habits of the worms; the "feet" of *Nereis* are well adapted for use in rapid crawling or in swimming, while the parapodia of *Arenicola* are more fitted to its burrowing habits. The two rami of the acirrate parapodia of *Arenicola* (Pl. XII, Fig. 39) are dissociated: they arise, not from a common basal piece, but directly from the body wall.

The notopodium, which is situated dorso-laterally, is a cylindro-

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conical elevation, and on or near its rounded end is the oval mouth of the chaetal sac, from which the tips of a pencil of chaetae[1] project. The chaetal sac traverses the axis of the notopodium and extends into the coelomic cavity. Fixed into the bottom of the sac are the numerous capillary chitinoid chaetae, moved collectively by special protractor and retractor muscles, which govern the extent to which the chaetae protrude. The notopodium is capable of considerable extension and retraction; in Pl. XII, Fig. 39, it is shown in a semi-contracted condition, its terminal part having been partially withdrawn into the basal portion. The notopodia are of a similar type throughout the genus and are present on all the chaetiferous segments, except in some examples of *A. branchialis*, in which the notopodia of the first segment are wanting.

The neuropodium is a muscular ridge traversed dorso-ventrally by a narrow slit—the mouth of the setal sac—from which the tips of a row of crotchets project. The section drawn (Pl. XII, Fig. 39) has passed immediately anterior to the chaetal sac, within which the inner ends of the crotchets are indicated. The muscular ridge and its hooked crotchets are excellently adapted for aiding the worm in its movements up and down its burrow; by their means one or more segments can fix themselves to the wall of the burrow, and the rest of the body can then be drawn towards this fixed portion by contraction of the longitudinal muscles. There are two types of neuropodia. In *A. pusilla* and *assimilis* the neuropodia form more or less oval, cushion-like pads on the lateral portions of the chaetiferous annuli; but, even in the posterior branchial region, where the neuropodia are best developed, they do not approach the mid-ventral line. In the other species of the genus the neuropodia are elongate muscular ridges, which, in the middle and posterior branchial segments, reach almost to the mid-ventral line. The neuropodia of the anterior segments (the first six or seven) are smaller than the rest, and in *A. cristata* neuropodia are not generally visible on the first two (sometimes three) chaetiferous segments.

The posterior segments of some specimens of *A. cristata* and *loveni* exhibit, between the notopodium and neuropodium, an oval depression not more than ·5 mm. in diameter (Pl. V, Fig. 13, and Fig. 44, p. 104). The position of these pits corresponds to that of the

[1] The chaetae are not simple hairs; they possess "Sägeblätter" (see p. 44), that is, series of spine-like processes. When the chaetae are pressed into the sand their processes offer resistance. These chaetae are thus more efficient than simple hairs would be in aiding locomotion.

"Seitenorgane" of other Polychaeta, but it has not been found possible to determine, on the material available, if the pits are really sensory structures.

The number of segments characteristic of each of the caudate species is, on the whole, constant, only very few variations having been observed. *A. cristata* and *glacialis* have 17 segments, *A. marina*, *pusilla*, *loveni* and *assimilis* var. *affinis* have 19 segments, while the typical form of *A. assimilis* has 20 segments.

In the ecaudate species there are considerably more segments, the full number of which—about 42 in *A. branchialis* and 64 in *A. ecaudata*—is already present at the end of the post-larval stage. The number of segments in these species does not increase with age, on the contrary, segments are usually lost posteriorly and are not regenerated, so that specimens are generally found to have fewer segments than stated above; average specimens of *A. branchialis* have about 30, and of *A. ecaudata* about 45 to 50 segments.

Each chaetiferous segment, except the first two or three, is subdivided into five rings,[1] and a consideration of the internal anatomy shows that the posterior limit of the segment is at the posterior edge of the ring which follows the chaetiferous one. Thus each of the segments, posterior to the third, consists of the chaetiferous annulus together with the three annuli in front of and that behind it. The third segment consists of three or four rings, the penultimate being chaetiferous; the second segment is generally subdivided into three rings, of which the middle one bears the parapodia. The first segment[2] is usually composed of two rings, the anterior of which is chaetiferous; in rare cases another small ring is present and lies in front of the chaetiferous annulus. The limits of these segments are ascertained chiefly by an examination of the internal septa, which are a constant feature of this region in all species of *Arenicola*.

Between the anterior margin of the first chaetiferous segment and the prostomium there is a region which, in most adult specimens of *Arenicola*, is subdivided by encircling grooves into three or four (or more) rings. There are good reasons for stating that this region is composed of the peristomium and a body-segment which is with-

[1] Occasionally the last one or two segments in *A. branchialis*, and the last one to four segments in *A. ecaudata*, are subdivided into fewer than five annuli.

[2] That is, the first chaetiferous segment. The word "segment" throughout the following pages means "chaetiferous segment."

out chaetae in the adult. In post-larval stages of *A. marina* (Pl. X, Fig. 27) and *ecaudata* (Pl. XI, Fig. 34) the region between the prostomium and the first ordinary chaetiferous segment is subdivided by a groove into two parts. The anterior and usually rather smaller portion is undoubtedly the peristomium; it never bears chaetae, but the paired statocysts may be seen near its anterior margin. The posterior of the two parts is, in the post-larval stages which the writer has examined, achaetous, but a chaeta has been observed in this segment, in either *A. marina* or *A. ecaudata*, by Professors Ehlers, Benham, Mesnil and Fauvel, a fact which demonstrates that this is a true segment.[1] In later post-larval stages, in which the annulation is making its appearance, the peristomium and the segment in question become subdivided into secondary rings, so that, henceforward, the segmentation of this region, like that of the rest of the body, is obscured; but it frequently happens that the original groove between the peristomium and the segment under consideration remains more obvious than any of those subsequently formed, and is recognisable even in the adult (Fig. 54, p. 118). Dr. R. S. Lillie[2] does not agree with the interpretation given above, because he could not find, in young *A. cristata*, a septum corresponding to the achaetous segment. But the considerable length and subdivision of, and the presence of two apparently segmental pigment-bands in, the region in question (Pl. X, Fig. 30) suggest that it includes the peristomium and another segment. The composition of this region is probably constant throughout the family.

In *A. ecaudata* and *branchialis* the parapodia are continued to the posterior end of the animal; but in *A. marina, pusilla, assimilis, loveni, cristata* and *glacialis* there is a "tail" in which parapodia and gills are not present. The tail is marked with a number of slight constrictions, which indicate the boundaries of the somites and correspond to internal septa. The number of tail-segments varies considerably in different individuals of the same species, because several segments, or even the major portion of the tail, may be thrown off on irritation.

During development, new chaetiferous segments are formed immediately in front of the terminal segment or pygidium. In the

[1] Evidence confirmatory of this interpretation is afforded by the arrangement of the giant nerve-cells (Ashworth, Liverpool Mar. Biol. Comm. Mem. xi (1904), p. 11).

[2] Mitt. Zool. Stat. Neapel, xvii (1905), p. 358.

ecaudate species all the segments are produced in this growing zone, the activity of which becomes exhausted about the end of the post-larval stage. In the caudate species, after the full number of chaetiferous segments has been formed, the succeeding or tail-segments are evidently produced at the anterior end of the tail; for in this region each segment is short from before backwards, while in the middle and posterior regions of the tail the segments are longer, and, in adult or late post-larval specimens, are subdivided into annuli. In *A. cristata* the full number of tail-segments—38 to 40—is acquired before the end of the post-larval stage. Examination of adult specimens of *A. marina* and *loveni*, however, indicates that new segments are continually being added to the tail at its anterior end, and, as a consequence, the number of tail-segments may become very large, *e.g.*, in the tail of an example of *A. loveni* there were 175 septa, indicating as many segments. In *A. marina* there may be 60 to 70 tail-segments, though usually there are fewer, owing to losses posteriorly.

In many of the tail-segments of all the caudate species of *Arenicola* there is one annulus slightly larger and more deeply pigmented than the rest, upon which distinctly larger epidermal papillae are borne. Each of these larger annuli occupies a position in the tail-segment corresponding roughly to that of the chaetiferous annulus in the pre-caudal segments of the worm.

Traversing the whole length of the mid-ventral line, in many specimens of *A. marina, pusilla, assimilis* and *loveni*, there is a shallow groove which marks the position of the ventral nerve-cord. A short distance in front of the first chaetiferous annulus this groove unites with the two metastomial grooves, which pass round the sides of the peristomium (metastomium), in an antero-dorsal direction, to the region of the prostomium (Fig. 53, p. 118). The metastomial grooves indicate the course of the oesophageal connectives. In other species the ventral and metastomial grooves are either faint or absent.

External Apertures.—The mouth, when the proboscis is withdrawn, is a crescentic or semicircular transverse slit in the antero-ventral region of the peristomium. It is overhung by a series of papillae, which belong to the peristomium and form the upper lip, dorsal and posterior to which the prostomium is situated. The anus is posterior and terminal.

The nuchal organ is a pro-curved, crescentic or U-shaped, ciliated

invagination at the junction of the prostomium and peristomium, and into it, in the caudate species, the prostomium may be withdrawn so as to be almost or quite hidden from view.

In *A. marina, assimilis* and *glacialis* the statocysts open to the exterior by pores situated on the dorso-lateral wall of the peristomium. In *A. marina* the pore[1] is present, on each side, near the point at which the metastomial groove crosses the first inter-annular groove (Pl. XII, Fig. 40). In *A. assimilis* the pore[1] is situated at the origin of the metastomial groove, that is, close to the prostomium on each side (Fig. 4). The position of the aperture in *A. glacialis* has not been definitely ascertained, but it is probably similar to that of *A. marina*.

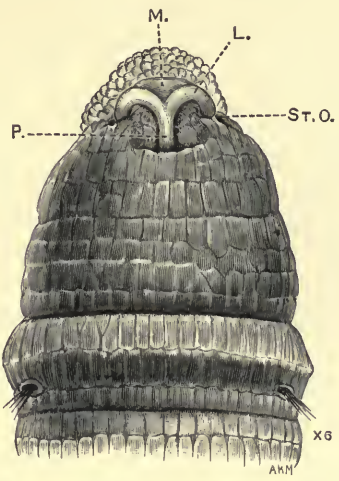

Fig. 4.—*A. assimilis* var. *affinis*. Anterior end, dorsal aspect; showing prostomium very fully protruded, exposing to view the median posterior part (P.), which is usually hidden in the nuchal organ; M. Median, L. Lateral lobe of prostomium; ST.O. External opening of statocyst.

The nephridial apertures are situated immediately dorsal and slightly posterior to the upper ends of the neuropodia of the segments on which they occur. In *A. marina, assimilis*[2] and *glacialis* the first nephridiopore is on the fourth segment, in *A. cristata, pusilla, loveni, branchialis* and *ecaudata* the first pore is on the fifth segment. There are six pores on either side in *A. marina, assimilis,*[2] *glacialis* and *cristata,* five in *A. pusilla, loveni* and *branchialis,* and thirteen in *A. ecaudata.*

Chaetae.

In adult specimens the notopodia never contain crotchets, but a crotchet, either alone or accompanied by one or more capillary chaetae, was observed by Prof. E. B. Wilson (1883) in the notopodia of larval *A. cristata,* and by Prof. Mesnil (1897) in specimens of "*Clymenides ecaudatus,*" afterwards shown to be post-larval speci-

[1] These apertures are minute, and can be seen only in those specimens in which the peristomial region is well extended.

[2] In examples of *A. assimilis* var. *affinis* from South Africa there are only five pairs of nephridiopores, the first of which is on the fourth segment.

mens of *A. ecaudata*. I also found crotchets[1] in the posterior notopodia of a post-larval *A. ecaudata*, 8 mm. in length. This

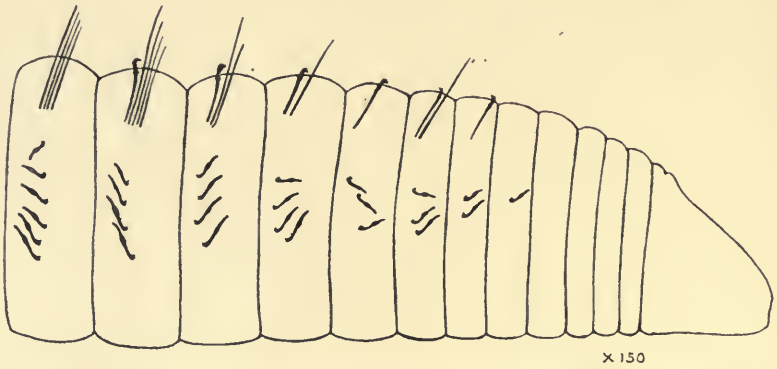

Fig. 5.—*A. ecaudata*. Outline of the posterior end of a post-larval specimen, 8 mm. long, to show the chaetae.

Fig. 6.—*A. ecaudata*. A crotchet from one of the posterior notopodia of the specimen shown in Fig. 5.

specimen has recently been subjected to further clearing, and this has rendered it possible to get a better view of the dorsal crotchets, which are not as short as they are drawn in the figure cited. Fig. 5 is a more accurate representation of this specimen and of its two types of crotchets, which are shown more highly magnified in Figs. 6, 28 (p. 56). Elongate crotchets, similar to that of Fig. 6, are present in the last five notopodia of post-larval examples of *A. branchialis*, 4·4 and 5·8 mm. long respectively.

I have examined a series of larval and post-larval *A. cristata* for notopodial crotchets, which are already present in larvae with four or five chaetiferous segments. A larva, ·7 mm. long, with ten chaetiferous segments (Fig. 7), bears in each of the last six notopodia a crotchet of the long type. In an older specimen, 2·6 mm. long, which has the full number (seventeen) of chaetiferous segments, only one notopodium, the penultimate, contains a crotchet; and in a specimen 3 mm. long crotchets are not present in any of the notopodia.

It is clear from these observations that a crotchet, differing from

[1] Figured in Q. J. Micr. Sci., xliii (1900), pl. xxiv, fig. 37.

those of the neuropodia in the greater length of its shaft, is present, but for a short time only, in a few of the last-formed notopodia of very young specimens. A notopodium never contains more than one crotchet, and after this has been cast out it is not replaced by a chaeta

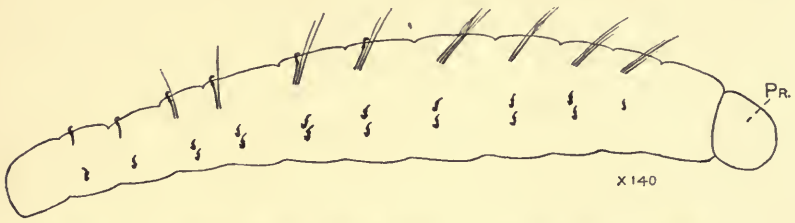

Fig. 7.—*A. cristata.* Outline of a larva, about ·7 mm. long, to show the chaetae. PR. Prostomium.

of a similar kind, but henceforward capillary chaetae only are formed in the notopodium. The evidence afforded by the young stages of *A. cristata* described above shows that, in this species, the crotchets are lost from the notopodium within a very short time of the attainment of the full number of chaetiferous segments. Probably this is also the case in other species, for in none of the notopodia of post-larval stages of *A. marina* (of which examples only 3·6 mm. long have been examined) or of *A. assimilis* has the writer been able to find a crotchet.

Notopodial Capillary Chaetae of Young Specimens.—The capillary chaetae successively present in any one notopodium exhibit a series of changes of form, the principal phases of which, traced chiefly in *A. pusilla*, *cristata* and *marina*, may be noticed here. Within twenty-four hours after hatching, the larva of *A. pusilla* or *A. cristata* acquires its first chaetae—a pair situated some distance behind the middle of its length. There are no elevations of the body-wall, that is, no actual notopodia, but the two chaetae indicate the position of the first notopodia. The free end of the chaeta (Fig. 8 A) is almost spoon-shaped, the shaft being continued, but tapered, along the axis of the flat "bowl" of the "spoon." In older larvae, with three or four segments, each notopodium contains a chaeta similar to that just described, but in each of the anterior two or three segments there

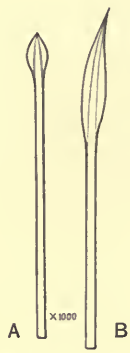

Fig. 8.—*A. pusilla.* A, First notopodial chaeta of a larva ·25 mm. long; B, Notopodial chaeta of an older larva with four chaetiferous segments.

Fig. 9.—*A. marina.* Notopodial chaetae of a post-larval specimen, 4·3 mm. long.

Fig. 10.—*A. ecaudata.* Distal halves of notopodial chaetae from post-larval specimens about 7 mm. long.

is also a chaeta, the free end of which is spear-like (Fig. 8 B). Spoon- and spear-headed chaetae are also present in the notopodia of young larvae of *A. cristata*, in which only two or three segments are indicated; but the spoon-shaped chaetae are soon cast out, and successive spear-headed chaetae, in which both shaft and head are of gradually increased length, are formed during the rest of the larval period. The tip of each of the later formed spears is drawn out into a long, fine point. In post-larval specimens there are all transitional forms, from spear-headed to laminate chaetae similar to those of the adult, as shown in Fig. 9, which represents chaetae from a post-larval *A. marina*, 4·3 mm. long. Each notopodium of this worm contains one chaeta of the type shown in Fig. 9 A, accompanied by from one to five of the longer capillary chaetae shown in Fig. 9 C. Fig. 9 B represents a form transitional between those represented in Figs. 9 A, C. Similar growth-phases are exhibited by the notopodial chaetae of post-larval *A. assimilis* var. *affinis*. The spear-headed chaetae probably do not persist long after the post-larval stage has abandoned its free-swimming habit, for, in a young specimen of *A. marina*, 17 mm. long, from the shore, spear-shaped chaetae were not present; the chaetae were all of the adult form, laminated along one margin only.

In post-larval stages of *A. ecaudata*[1] there are two kinds of capillary chaetae—(1) long tapering chaetae, similar to the majority of those seen in late post-larval *A. marina*, and (2) shorter chaetae of the kind shown in Fig. 10 B, noteworthy for the presence of a slight constriction about the junction of middle and distal thirds. A few chaetae, like that shown in Fig. 10 A, are transitional forms succeeding spear-headed chaetae of earlier stages of development.

These observations indicate that, throughout the genus, there is a sequence of growth-forms of the notopodial chaetae, from spoon- and spear-headed early phases to tapering chaetae, which alone are found in the adult.

The Notopodial Chaetae of Adult Specimens.—Each notopodial chaeta of an adult specimen is a yellow or golden, slender, chitinous, tapering structure. It is inserted at its thicker, proximal end, along with a number of similar chaetae, in a chaetal sac, which is moved by protractor and retractor muscles (p. 35). The differences between the chaetae of the various species consist in the presence or

[1] Also of *A. branchialis*, though these have not yet been as fully studied.

absence of a lamina along the distal portion, and in the nature and comparative abundance of the processes present in that region of the chaeta.

The most highly developed notopodial chaetae present in the genus are found in *A. loveni*. In the notopodia of this (and some other) species the chaetae seem to be in two more or less distinct series, an anterior and a posterior; the chaetae of the anterior are shorter than those of the posterior row, but they have the same form and structural detail. The longer chaetae are about 6·6 to 6·8 mm. long, and the shorter ones 5·3 to 5·6 mm. Each has a moderately uniform diameter for the greater part of its length, but in its distal portion tapers to a fine point. For a distance of 1 to 1·3 mm. behind the tip, there is, along one edge of the chaeta, a well-marked lamina (Fig. 11 A), which attains a breadth of 15 μ and, as seen under medium magnification, is marked by closely set oblique lines and has a finely dentate margin. The opposite edge of the chaeta bears numerous regularly arranged processes, which, under low or medium magnification, appear as fine teeth projecting at an angle of about 30° to 40° from the shaft of the chaeta, but which, examined with an immersion lens, are seen to be crests passing round the shaft (Fig. 11 B). The undivided base of each crest is fixed to the shaft, and the distal portion of the crest, that is, its free margin, is subdivided into a large number of fine teeth. Each crest appears to be a comb-like structure, bent so as to envelop the greater part of the shaft of the chaeta, the curved portion of the crest being seen in profile where it projects from the shaft. The regularly arranged structures visible, under low power, as fine teeth along one margin of the chaeta are, then, the crests seen in profile, and

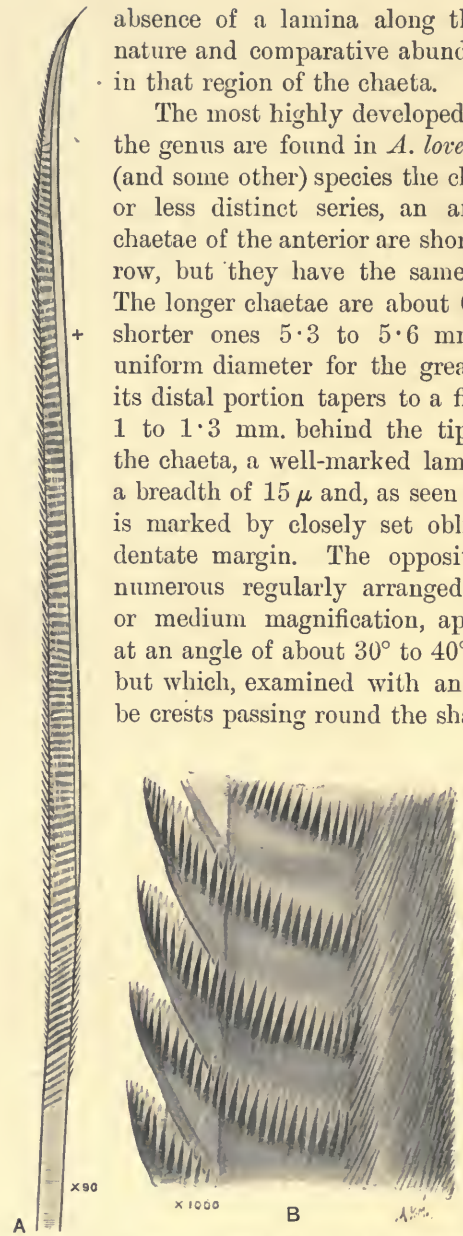

Fig. 11.—*A. loveni*. A, Distal third of a notopodial chaeta, from a specimen 335 mm. long; B, The region marked + in A more highly magnified.

these remind one of the similar crests or "Sägeblätter" of the chaetae of some Aphroditidae and certain other Polychaeta. The laminate portion of the chaeta bears on its surface numerous fine processes, the pointed tips of which are directed at slightly different angles; those viewed in profile at the margin of the lamina form a regular series of very fine teeth. In each interval between the "Sägeblätter" there is a denser transverse band, the presence of which, at regular distances of about 10 to 12 μ, gives to the distal portion of the shaft of the chaeta a transversely striated appearance, which is seen clearly even under low magnification (about 50). This well-marked striation and the great development of the crests on the shaft are two characteristic features by which the chaetae of *A. loveni* may be distinguished from those of any other species of *Arenicola*.

The notopodial chaetae of other species apparently all possess crests of a similar type to those of *A. loveni*, but of more feeble development. The crests break up into their individual teeth and the latter become spread, by use, in different directions, so that the shaft of the chaeta is covered, to a greater or less extent in different species, with numerous hair-like or spine-like processes, the association of which with one another to form comb-like crests, is, in many cases, no longer obvious.

The chaetae of young specimens (up to about 48 mm. long) of *A. cristata* are laminate along one side for a short distance, but the lamina is markedly dentate and soon breaks up into teeth. In older examples the chaetae, even when newly formed, are non-laminate. The tip of an unworn chaeta, from a specimen 280 mm. long, is represented in optical section in Fig. 12 A. The chaetae of this species, when the tip has been worn away by use, present the appearance shown in Fig. 12 B. In large examples, in which the chaetae attain a length of 9 mm., the spinous processes (teeth of the Sägeblätter) are very numerous. The chaetae of *A. glacialis* resemble those of *A. cristata*, but are rather less spinous.

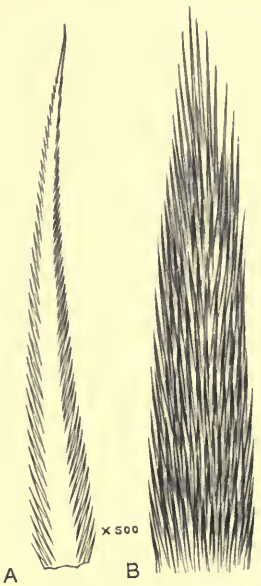

Fig. 12.—*A. cristata*. A, Tip of an unworn notopodial chaeta, seen in optical section, from a specimen 280 mm. long; B, End of a worn chaeta, from a specimen 400 mm. long.

The chaetae of *A. marina*, *pusilla* and *assimilis* possess, along one side of their distal fourth or fifth, a thin lamina, which, in large

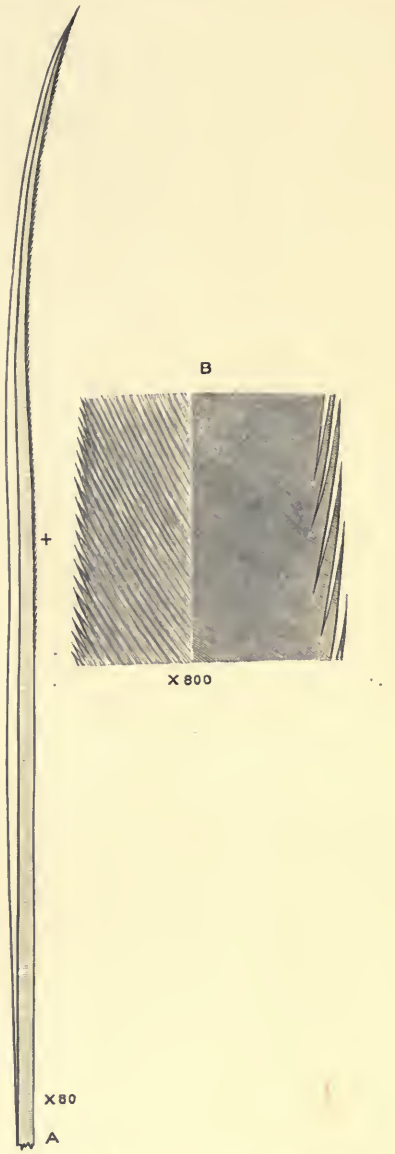

Fig. 13.—*A. marina* (250 mm. long). A, Distal fourth of a notopodial chaeta ; B, The region marked + in A more highly magnified.

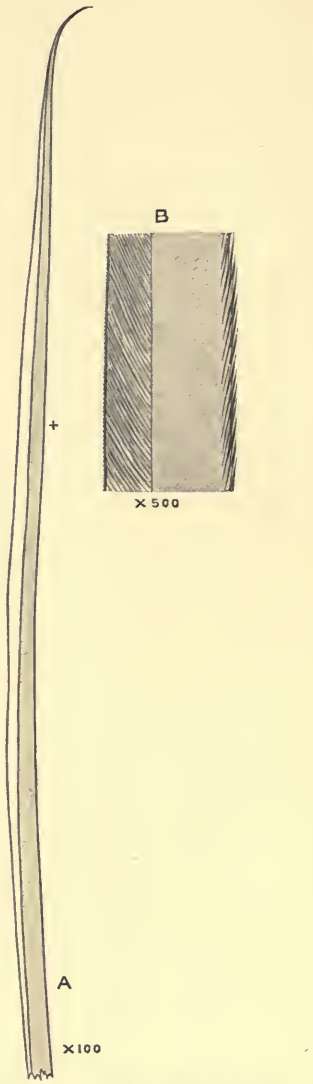

Fig. 14.—*A. assimilis* var. *affinis* (250 mm. long, from Otago Harbour, N.Z.). A, Distal third of a notopodial chaeta ; B, The region marked + in A more highly magnified.

chaetae, may attain a width of 15 to 20 μ. The lamina may be entire at its margin, and crossed by numerous fine oblique lines, or it may be breaking up, from the edge inwards, along the course of the oblique striae, so that its margin becomes denticulate. On the opposite side of the chaeta and pressed closely to the shaft, are Sägeblätter, the spines of which are smaller than in *A. cristata*.

Fig. 15.—*A. pusilla*. The end of a fractured chaeta, from a large specimen from Unalaska.

Figs. 13 A, B (the latter an optical section) are drawn from the chaetae of *A. marina*, but the figures would serve also for some specimens of *A. assimilis*. The chaetae of the latter species are, however, usually rather less hairy and the spines are smaller (Fig. 14) than those of *A. marina*, but examples from different localities have been found to exhibit variation in this respect. Chaetae of *A. pusilla* also present considerable differences in the degree of their "hairiness," some closely resemble those of *A. marina*, than which, however, they are usually rather less hairy. The fractured end of a large chaeta, from a massive example of *A. pusilla*, is represented in Fig. 15, and shows the Sägeblätter; the figure would serve almost equally well for a chaeta of *A. marina*.

The chaetae of *A. ecaudata* and *branchialis* are identical in form and characters. Although they are as stout basally as chaetae of the same length from the caudate species, they begin to taper nearer to the proximal end, and their distal portion is consequently more slender. The newly formed chaetae of

Fig. 16.—A, *A. ecaudata*. Distal half of a notopodial chaeta, seen in optical section. B, *A. branchialis*. Tip of a notopodial chaeta, surface view.

the ecaudate species have, along one side, a narrow lamina (2 to 4 μ wide), which, however, soon breaks up into fine teeth (see the left proximal portion of Fig. 16 A). The opposite side of the chaeta bears longer spines. Towards the tip the shaft of the chaeta appears to be encircled by series of spines (Sägeblätter), which can be resolved only with difficulty (Fig. 16 B).

The only species of *Arenicola* in which the notopodial chaetae present characters sufficiently striking and definite to be of real service in systematic work is *A. loveni*, the chaetae of which are distinguished by their well-developed Sägeblätter, and the transverse striation of their distal portion. The notopodial chaetae in the case of a specimen of any other species would serve, at most, to indicate to which of three groups—*marina-pusilla-assimilis*, *cristata-glacialis*, *ecaudata-branchialis*—the specimen belonged.

Neuropodial Crotchets.—The successive generations of crotchets exhibit progressive changes which, although small, result in the end terms of the series being of markedly different form, that is, the crotchets of the larval and post-larval stages differ widely from those of the adult.

A. marina.—The crotchets of a post-larval specimen of *A. marina*, 5 mm. long, have the form shown in Fig. 17. The proximal end of the shaft is fixed to the bottom of the setal sac and the greater part of the length of the shaft, up to and including the well marked dilatation present upon it, is enclosed in the sac. The distal portion of the crotchet is bent almost at a right angle to the shaft and forms a beak-like structure—the rostrum. Immediately proximal to the rostrum, on the convex (*i.e.* ventral) side of the curvature of the crotchet,[1] there are three (or four) teeth, of which that nearest the rostrum is the largest. On the shaft, just under the rostrum, there is generally visible a small pointed process—the sub-rostral process—which is more highly developed in some crotchets than in others. Careful focussing shows that the series of teeth is continued round the sides of the rostrum, and that the sub-rostral process is the expression of the smallest of these; thus the rostrum projects from a series of teeth encircling its base. This is more clearly seen in the crotchets of post-larval stages of *A. assimilis* (Fig. 21, p. 50) and also in the adult crotchets of certain species, *e.g. A. branchialis* (Fig. 30, p. 57).

Fig. 17.—*A. marina*. Crotchet from a post-larval specimen, 5 mm. long.

[1] The position of the crotchets in the neuropodium is shown in Pl. XII, Fig. 39.

A crotchet from a young *A. marina*, 17 mm. in length, which had assumed the adult form and mode of life, is shown in Fig. 18. The teeth are proportionately smaller, and the rostrum is placed at a greater angle to the shaft—about 120°, instead of about 90° in the younger crotchet of Fig. 17. Specimens about 100–130 mm. long have crotchets of the form shown in Fig. 19; there are four or five minute teeth behind the rostrum, which latter is placed at an angle of about 135° to the shaft.

Fig. 18.—*A. marina*. Crotchet from a young adult, 17 mm. long.

Crotchets from very large specimens have a markedly elongate rostrum, still more nearly in line with the shaft, and are entirely without teeth. The absence of teeth is not due to their having been worn away by use, as may be shown by isolating the entire series of crotchets and selecting for examination those which have not yet come into use at the ventral end of the series. The ventral portion of such a preparation is shown in Fig. 20. The tip of the crotchet on the left is projecting from the lip of the chaetal sac, the outline of which is shown, and would soon have come into use.[1] Various stages in the formation of crotchets are seen, and it will be noted that teeth are not developed. New crotchets are being constantly produced at the ventral end of the series and the old, worn ones cast out at the dorsal end of the chaetal sac. Occasionally small relict crotchets are found in the bottom, and usually near the dorsal end of the chaetal sac, from which they should have been cast along with their contemporaries, but for some reason—probably entanglement in the tissue or mucus—they have been retained.

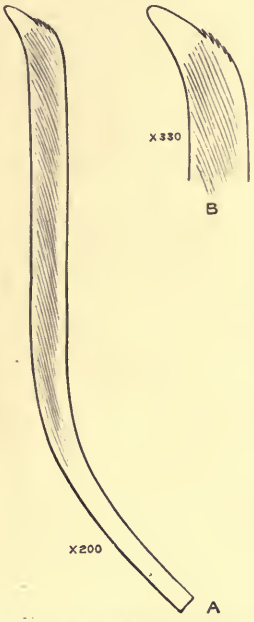

Fig. 19.—*A. marina*: A, Crotchet from a specimen 125 mm. long; B, Tip of another crotchet from the same specimen.

The principal changes in the crotchets of *A. marina, pari passu* with the increase in size of the worm, are (1) increase in size and

[1] This chaetal sac contained 117 other crotchets, practically identical in size and form with that shown on the left of the figure.

number, (2) gradual reduction and eventual loss of the teeth behind the rostrum, (3) increase of the angle between the rostrum and shaft, and (4) elongation of the rostral region, which is seen only in crotchets from very large specimens. The crotchets of other species of *Arenicola* exhibit corresponding changes.

A. assimilis.[1]—Crotchets from a post-larval example of the var. *affinis*, 7·6 mm. long, are shown in Fig. 21. The left one is drawn with the rostrum almost in optical section; the right one, which is shown

Fig. 20.—*A. marina* (250 mm. long). The ventral end of a neuropodial chaetal sac, showing the formation of crotchets.

Fig. 21.—*A. assimilis* var. *affinis*. Crotchets from a post-larval specimen, 7·6 mm. long.

with the surface of the rostrum focussed, demonstrates that the series of teeth extends round the base of the rostrum, and that the sub-rostral process is the lowest and smallest of the series. Fig. 22 A represents a crotchet, from a specimen 136 mm. long. This is similar in form to that of *A. marina* (Fig. 19), and does not present any dilatation of the post-rostral region (contrast the crotchets of

[1] The neuropodia of *A. assimilis* and *pusilla*, being much shorter than those of *A. marina*, contain fewer crotchets; an average number, in specimens about five inches long, is 30 to 40 in each neuropodium of the branchial region.

A. pusilla, Fig. 24). A crotchet from a specimen of *A. assimilis* var. *affinis*, 208 mm. long, is drawn in Fig. 22 B. It is 1·1 mm. in length, and its characters—the elongate edentulous rostrum (a little worn at the tip) making a wide angle with the shaft—are such as would be expected in a crotchet from so large a specimen.

A. glacialis.—The crotchets of this species are similar in general form to those of *A. marina*, and have no post-rostral dilatation (Fig. 23). A neuropodium of one of the fragmentary type specimens yielded large crotchets of the type shown in Fig. 23 C, in which the rostrum is longer and is curved almost like the blade of a scythe. This represents probably the final growth-phase.

A. pusilla.—The crotchets of this species exhibit a full rounded curvature of the region behind the rostrum, so that the free end of the crotchet resembles the head and beak of a swan. This character is shown best in small or medium sized specimens (Fig. 24 A, B), and is especially marked in the crotchets of the type specimen (Fig. 24 B). It is also obvious, but to a less degree, in the large crotchets (Fig. 24 C), which represent the latest growth-phase seen by the writer, of a massive specimen 160 mm. in length.

The head-like curvature is more strongly marked in this species than in *A. cristata*. As *A. pusilla* is one of the most difficult species to identify, this character is of considerable value, for in the two species with which *A. pusilla* is most easily confused, namely, *A. marina* and *assimilis* var. *affinis*, the crotchets do not present any dilatation of the post-rostral portion.

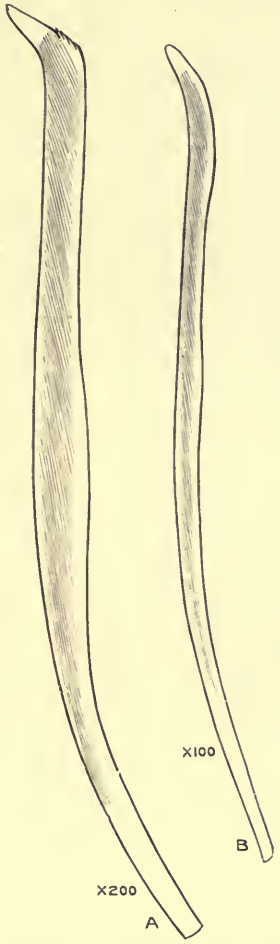

Fig. 22.—*A. assimilis* var. *affinis*. A, Crotchet from a specimen 136 mm. long, from Otago Harbour, N.Z.; B, Crotchet from a specimen 208 mm. long, from Kerguelen.

A. cristata.—The sequence of growth-phases (Figs. 25, 26) has been found to be similar to that described for *A. marina*. In crotchets (Fig. 26 D, E), which show the final phase of growth, from

a massive Floridan example 330 mm. long, the shaft and rostrum are practically in line, and merge into each other. The tip of the rostrum, shown in Fig. 26 E, which represents the end of a newly-

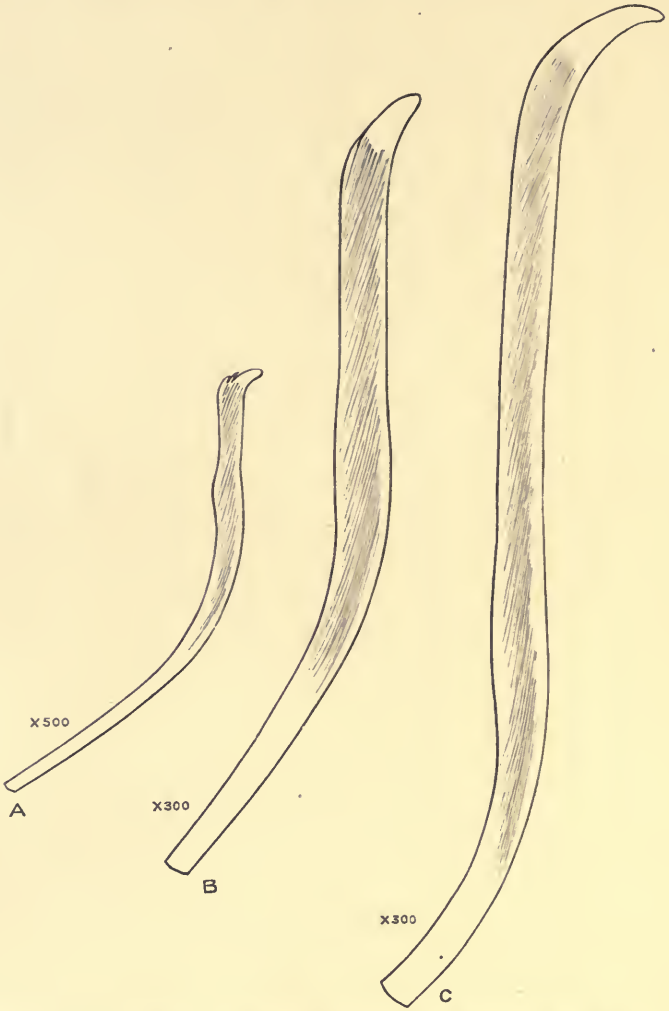

Fig. 23.—*A. glacialis.* A, Young crotchet ; B, Later phase ; C, Latest phase of growth found.

formed, unused crotchet, soon wears away, leaving a rounded end (Fig. 26 D).

The crotchets of *A. cristata* are intermediate between those

of *A. marina* and *pusilla* in the form of their post-rostral region.

A. loveni.—Crotchets of large examples only, exhibiting late growth-characters, are available (Fig. 27, A from the type specimen and B from a similar specimen collected in Saldanha Bay). They are intermediate in their characters between those of *A. marina* and *cristata*, but are, on the whole, rather nearer those of the latter species.

A. ecaudata and *branchialis.*—The crotchets of these two species are practically identical in size and form. They do not attain so great a size as the crotchets of the caudate species; for they appear not to exceed ·4 mm. in length, whereas in large examples of *A. loveni* the crotchets attain a length of ·8 mm., in *A. marina* and *cristata* ·9 mm., and in *A. assimilis* and *pusilla* 1·1 mm.

A crotchet from a post-larval *A. ecaudata*, 8 mm. long, is shown in Fig. 28, and presents the usual characters found in small crotchets. Fig. 29 represents two crotchets from the same neuropodium of an adult *A. ecaudata* 200 mm. long. There were in this neuropodium 120 crotchets, of which the small one was the most dorsal and was about to be cast out, while the large one was just coming into use at the ventral end of the series. There is not usually so much difference in size between the extreme crotchets in the neuropodia of *A. branchialis*. The rostrum of the crotchets of both these species

Fig. 25.—*A. cristata.* First crotchet of a larva ·25 mm. long.

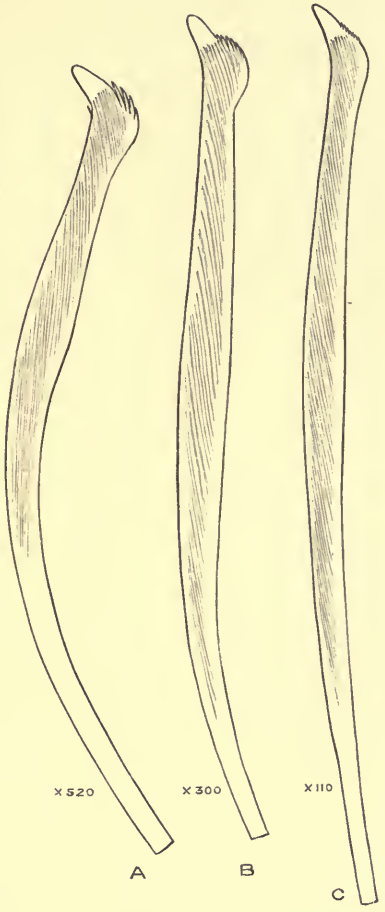

Fig. 24.—*A. pusilla.* A, Crotchet from a Neapolitan specimen, 17 mm. long; B, From the type specimen; C, From a large specimen, 160 mm. long, from Unalaska.

has, when unworn, a slender and slightly upturned tip (Fig. 29), which, however, is soon worn away when the crotchet comes into use. Fig. 30 represents the latest growth-phase found in the crotchets of these species.

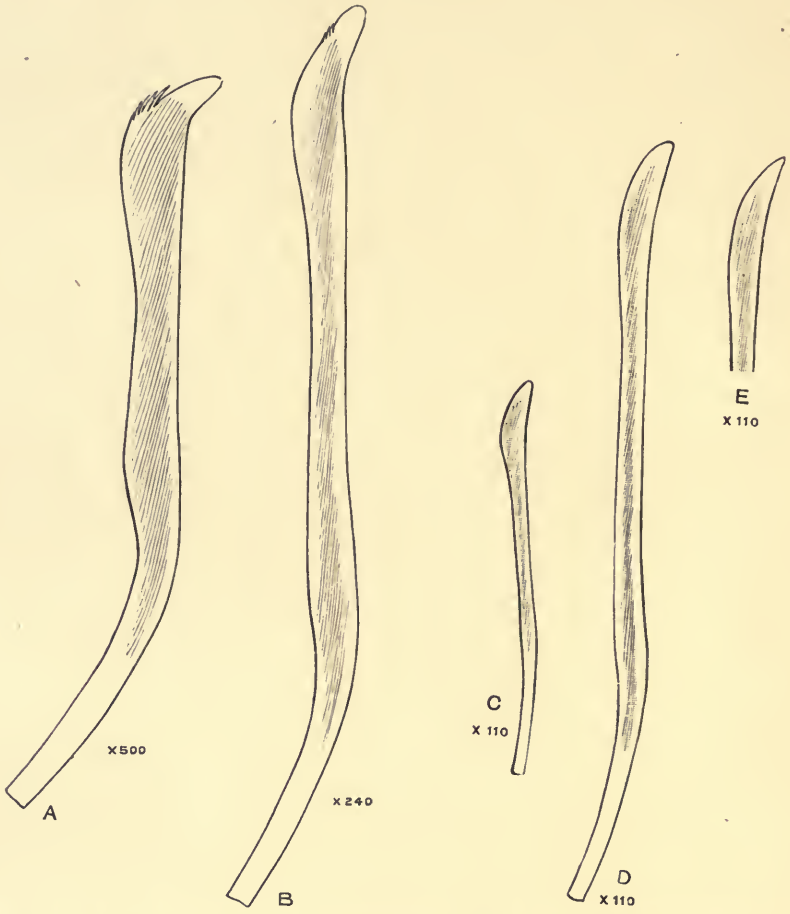

Fig. 26.—*A. cristata.* A, Crotchet from a young adult, 48 mm. long; B, From a specimen 130 mm. long; C, From a specimen 250 mm. long; D, A worn crotchet, and E, The tip of an unused crotchet, from a specimen 330 mm. long.

The crotchets of the larval and post-larval stages do not afford any reliable help in diagnosis, their form and characters seem to change so rapidly during the very early phases of growth that larval or post-larval crotchets of the same species, but of different

ages, may present differences as great as those between crotchets from different species but of about the same age. But soon after the worm has settled down to its littoral habit the crotchets assume the form characteristic of the species, and, henceforward, change only gradually and in a definite manner (see p. 49).

Among the caudate species the crotchets of *A. pusilla* are most readily recognised by reason of the full rounded curve of their post-rostral region, giving the free end of the crotchet the appearance of a swan's head and beak. The crotchets of *A. marina, assimilis* and *glacialis,* which present no dilatation of their post-rostral portion, are so closely similar that their aid cannot be invoked in separating these species from one another, but they may be of use in distinguishing this trio from the remaining species. The crotchets of *A. cristata* are intermediate, in the form of their post-rostral region, between those of *A. marina* and *pusilla,* and those of *A. loveni* are intermediate between those of *A. marina* and *cristata.*

Gills.

The gills are paired hollow outgrowths of the body-wall, situated immediately posterior to the notopodia in certain segments. They do not arise, in *A. marina,* until after the full number of chaetiferous segments, and a considerable number—about thirty—of tail-segments have been developed. The first indication of the formation of gills is seen in the penultimate and two or three preceding chaetiferous segments, in which, behind each notopodium, the segmental blood-vessels form a well-marked loop, over which there arises a slight elevation of the body-wall—the incipient gill (*cf.* Pl. X, Fig. 30). The gills of these segments become successively conical, digitiform and branched, and, meanwhile, gills make their appearance on the last and on the more anterior segments until the full number (thirteen pairs) has been attained. The gills are, from their earliest stage of formation, respiratory structures; there is no evidence that they are modified cirri.

The gills of *A. cristata* arise in a similar manner and sequence; they first make their appearance in young examples, about 5 mm. in length, which have the full number (seventeen) of chaetiferous and about twenty tail-segments.

In *A. ecaudata* also, the gills do not arise until the worm has almost attained its full number of segments. When the worm possesses about sixty fully formed segments, the formation of gills

may be looked for, in the first instance on the sixteenth to nineteenth segments inclusive. Subsequently gills are formed on the succeeding segments, but a considerable period elapses before the posterior segments acquire their branchiae; for instance, in a specimen 15 mm. long, with sixty-four segments, the last twenty segments are still abranchiate.

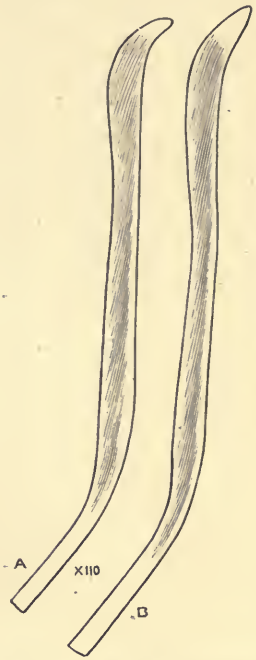

Fig. 27.—*A. loveni.* A, Crotchet from the type specimen; B, From a similar specimen from Saldanha Bay.

The gills are well supplied with blood-vessels and are, therefore, generally red in colour, but in old specimens they become pigmented, assuming a dark brown colour. They are sensitive and, on stimulation, usually contract, their red colour disappearing almost entirely. Specimens intended for the study of gills should be narcotised before being killed—successive small quantities of absolute alcohol being placed on the surface of the water in which they are living—so that the gills may remain in an extended condition. In specimens which have been suddenly plunged into the killing fluid, especially strong alcohol, the gills are so much contracted that their mode of branching is difficult to determine. In occasional specimens the gills have lost some of their branches either by friction against the sand or owing to the attacks of enemies, *e.g.* certain Crustacea.[1]

Fig. 28.—*A. ecaudata.* Crotchet from a post-larval specimen, 8 mm. long (see Fig. 5).

Each gill exhibits a number of main stems which radiate, in the ecaudate species, from a common basal trunk, or, in the caudate species, from a crescentic fold, immediately behind the notopodium. In some cases the crescentic fold is of considerable extent and forms, for instance in *A. marina*, a web-like membrane between the bases of the gill-axes. In the other species in which it occurs, this "web" is not by any means a constant character, for instance, it is present in examples

[1] *See* D'Orbigny, in Journ. Physique, xciii (1821), p. 198, for an account of the attacks of the Amphipod *Corophium longicorne* (now called *C. volutator*) on *Arenicola* and other worms.

of *A. assimilis* from New Zealand, but has not been found in those from other localities.

The dorsal axes of each gill are almost invariably the largest and evidently the oldest, judging by the number of their branches; new axes are added to the gill ventrally (see Pl. XIII, Fig. 43).

Gills are not present in the genus *Arenicola* on the first six segments; out of some thousands of specimens the writer has seen

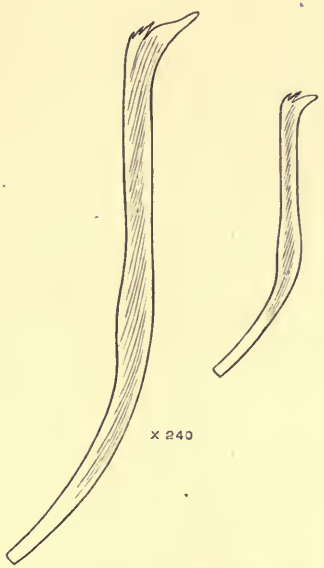

Fig. 29.—*A. ecaudata.* The dorsal (small) and ventral (large) crotchets of the same neuropodium of a specimen 200 mm. long.

Fig. 30.—*A. branchialis.* Crotchet from a specimen 230 mm. long.

only one in which a gill—a very small one—was present on the sixth segment.[1] In *A. marina, pusilla, assimilis* var. *affinis, loveni, cristata* and *glacialis* the first gill is normally on the seventh segment, in *A. assimilis* (typical form) on the eighth segment, in *A. branchialis* on the twelfth, and in *A. ecaudata* on the sixteenth. In *A. marina, pusilla, loveni* and *assimilis* (including the variety) there are thirteen pairs of gills; in *A. cristata* and *glacialis* eleven pairs; in *A. branchialis*

[1] One of Ranzani's specimens of *A. clavatus* (= *marina*) possessed a small gill on the sixth segment.

and *ecaudata* the number varies in different specimens, the maximum number seen in the former species is thirty pairs, and in the latter forty-seven pairs.

In all the species the first gill is almost invariably small, and, in a considerable percentage of examples, is reduced to minute proportions or is absent. The gills extend generally to the posterior end in adult ecaudate examples: but from one to nine segments in *A. ecaudata*, and from one to four in *A. branchialis*, may be gill-less.

In the caudate species of *Arenicola* there are two different types of gills, the pinnate and the fruticose (or bushy). In most specimens the gills are readily referred to one or other of these types, but, occasionally, it is difficult to state to which of the two forms the gill belongs, that is, the two types merge into each other. In the pinnate type the gill-axes are elongate, and along the sides of each axis there are numerous—ten to twenty—opposite or alternating branches placed at regular intervals, producing a pinnate appearance. The subsequent division of the lateral branches is either dichotomous, or, especially in the case of the larger ones, pinnate; the ultimate branches form the finger-like gill-filaments. The fruticose gill has shorter axes, each of which bears few (three to six) lateral branches on each side; these branches are closely set or irregularly placed, and they do not subdivide in a pinnate manner, but dichotomously, or in such a manner that the ultimate branches, that is, the gill-filaments, form a cluster. The collective effect of the massing together of, say, eight or ten axes, similar to that described, is to give the gill the appearance of a dense bush.

The gills of *A. cristata* are invariably of the pinnate type. Those of a specimen 175 mm. long are selected (Pl. XIII, Figs. 41, 42) as an average example of their size and condition in this species. The first and smallest gill consists of eight axes, of which that shown in Fig. 41 is the most dorsal and largest. It is 2·8 mm. long and bears nine branches on each side. Owing to the shortness of these branches their mode of subdivision seems to be somewhat irregular; some of them dichotomise, while others subdivide almost at once into a cluster of gill-filaments. The largest gills of the same specimen are composed of about fourteen or fifteen axes. The dorsal axis, 7·5 mm. long, of such a gill is shown in Fig. 42. The lower and middle branches are subdivided freely, often in a pinnate, sometimes in a dichotomous manner, and their terminal filaments lie, for the most part, in one plane. In the figure these branches are represented as seen in full view, but they actually lie in a plane almost at right

angles to that in which they are drawn. This gill-axis and the three hundred gill-filaments it bears, affording a very large aerating surface, would be a most efficient respiratory structure.

All the known examples of *A. loveni* possess typically pinnate gills, practically identical in their form and details with those of *A. cristata.*

Both types of gill are found in *A. marina.* The large Laminarian form has pinnate gills similar to those of *A. cristata;* the smaller littoral form has fruticose gills.

The second gill of a littoral example of *A. marina*, 120 mm. long, is shown in Pl. XIII, Fig. 43. The gill consists of nine axes, "webbed" at their base, and a tenth is just making its appearance. The longest—dorsal—axis is about 2 mm. in length, and its lateral branches are

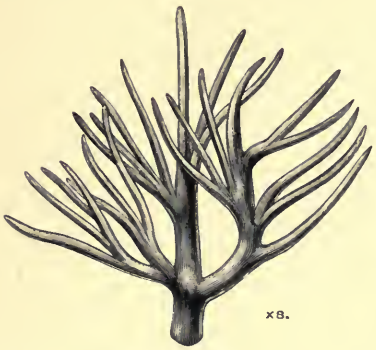

Fig. 31.—*A. marina* (from Wood's Holl), dorsal axis of fifth gill.

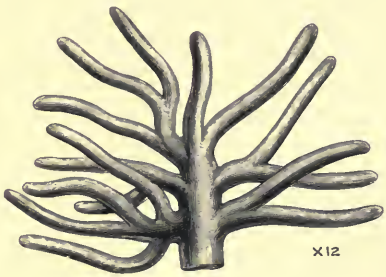

Fig. 32.—*A. pusilla* (from Unalaska). Dorsal axis of fifth gill.

typical of those found in this form of gill. The ventral axis is a little unusual in that one of its branches is disproportionately large.

A gill-axis from a specimen of *A. marina* (200 mm. long) from Wood's Holl, exhibiting a rather extreme form of the bushy type, is shown in Fig. 31. The lateral branches are few and are subdivided into a comparatively small number of very long filaments. The presence of eleven or twelve such axes, of which the gill is composed, in an area about 9 × 6 mm., produces the effect of a dense bush.

The gills of nearly all the specimens of *A. pusilla* examined conform to the pinnate type (*cf.* Pl. XIII, Fig. 41). Those of massive examples (160 mm. long) of this species from Unalaska are, however, of different form (Fig. 32): the axes are proportionately very short (2·5 mm.) and bear on each side only three, or at most four, branches,

and these are subdivided into only two to four gill-filaments. These gills have therefore a bushy appearance.

The gills of *A. assimilis* and of the examples of the var. *affinis* from Auckland Island are similar to those of the littoral form of *A. marina*, from which they differ only in the absence of "webbing" at the base of the gill-axes. The gill-filaments of most of the specimens examined are elongate, almost as long relatively as those shown in Fig. 31. Examples of *A. assimilis* var. *affinis* from New Zealand, the Falkland Islands and South Africa have pinnate gills.

A. glacialis has small gills, which present an extreme form of the bushy type. The axes even of the largest gills are not more than 2 mm. long. The most fully expanded gill found on any of the specimens is shown in Fig. 33. It consists of nine or ten axes, which arise from a short, curved, common basal structure situated immediately behind

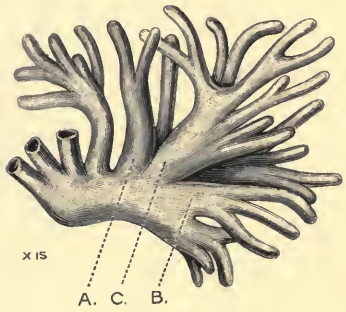

Fig. 33.

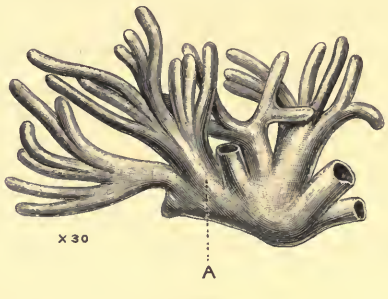

Fig. 34.

Figs. 33, 34.—*A. glacialis*. Two gills from different specimens. A few gill-axes have been cut away to afford a better view of the rest.

the notopodium. The longest axis (C) bears five forked branches; of the resultant gill-filaments the longest are thumb or finger-shaped and not more than ·7 mm. in length, and the shortest are mere tubercles. The smaller axes of this gill bear only two or three branches, which may be simple, that is, undivided distally (A, B). A well expanded gill from another specimen is represented in Fig. 34. It is smaller than that just described, the largest of the seven axes of which it is composed being scarcely 1 mm. in length from its base to the tip of its filaments. This axis (A) consists of three main stems, each of which bifurcates, and one of the two so formed again divides, but the other does not. In this manner, three groups, each of three gill-filaments, are clustered at the end of the axis. In all the gills examined the branches borne by an axis are clustered at the end, the result of the great abbreviation of the axis. *A. glacialis* and

cristata, both of which have eleven pairs of gills, are the extreme terms in the gill-series: in the former the axes are reduced and the branches clustered, in the latter the axes are elongate, and have numerous pinnately arranged branches.

The gills of the two ecaudate species, *A. ecaudata* and *branchialis*, which are identical in form, differ markedly from those of the caudate species. One of the smaller gills of a Neapolitan example of *A. branchialis* (76 mm. long) is shown in Fig. 35. Arising from a short common trunk are three stems about 1 mm. long, each bearing three branches, which are given off on one side only. The subdivisions of these branches are similarly restricted to one side, and the division is invariably dichotomous. The larger gills of the same

Fig. 35.—*A. branchialis*, entire gill.

Fig. 36.—*A. ecaudata*. Dorsal gill-stem. The gill had four other stems similar to this, all united at their bases.

specimen have four or five main stems with more numerous branches. A careful examination of many gills gives one the impression that the stem is not a true axis but a sympodium. A dorsal gill-stem of a British example of *A. ecaudata* (190 mm. long), represented in Fig. 36, exhibits the same mode of branching.

Coelom and Coelomic Septa.

The coelom is spacious and continuous from one end of the animal to the other. In front it is traversed by three transverse septa placed at the anterior boundary of the first, third and fourth chaetiferous segments respectively. These septa are present in all species of the genus.

The first septum is the strongest, for a portion of the pharyngeal

musculature has become associated with it. In all the species, except *A. pusilla* and *assimilis*, this septum bears two backwardly directed muscular pouches which lie to the sides of, and ventral to, the oesophagus (Pl. XIII, Fig. 46), and open into the coelomic space in front of the septum. The function of the pouches is unknown, but it has been suggested that they may be of use in aiding the eversion of the proboscis. The relative size of these pouches is practically constant in the members of the same species, but varies considerably in the different species; the grade of development of these structures, therefore, forms a useful systematic character. Septal pouches are not represented, even as vestiges, in *A. pusilla* and *assimilis;* in *A. marina* and *glacialis* they are small, conical or thumb-shaped structures, only about 2 to 3 mm. long in full grown specimens. The pouches of *A. ecaudata* and *branchialis* are finger-like, extend backwards almost as far as the second septum, and, in large specimens, are 5 to 8 mm. long. Those of *A. cristata* are usually of similar shape and length, but in very large American specimens they attain a length of 13 mm. The septal pouches reach the highest grade of development in *A. loveni*, in large examples of which they are 25 to 26 mm. long and about 3 to 4 mm. in diameter at their widest part (Pl. IV, Fig. 11). They extend backwards through apertures in the second septum, so that their blind ends lie against, or almost touching, the third septum. The enormous size of the septal pouches is the most striking feature in a dissection of this species.

The second and third septa are more extensive than the first but much thinner; they are fenestrated and permit the passage of the coelomic fluid and corpuscles.

From the third septum, that is, the anterior end of the fourth segment, backwards to about the fifteenth segment the body-cavity is uninterrupted by septa, but about the latter region vestigial septa may be recognised as strands of connective tissue of greater or less width accompanying some of the afferent and efferent branchial vessels. In the succeeding segments the septa are more perfect, and in the nineteenth segment, if not earlier, form easily recognisable, and, at first sight, complete partitions. These septa, which are not usually fenestrated, are, however, incomplete ventrally, that is, above the nerve-cord, and possibly also mid-dorsally. They are well seen in *A. ecaudata* and *A. branchialis*, and are present, though demonstrable with some difficulty, in the tail region of the caudate species, where they correspond in position with the inter-segmental grooves present on the external surface.

Alimentary Canal: Burrowing.

The alimentary canal presents an almost uniform structure throughout the genus, but the associated glands—the oesophageal caeca—exhibit certain differences which are of value in diagnosis. The canal consists of (1) an eversible buccal mass and pharynx; (2) a cylindrical oesophagus, often transversely wrinkled, which pierces the three septa, and, a short distance behind the level of the last of these, bears two or more oesophageal glands; (3) the "stomach," which is covered with yellow cells, gradually merges, about the level of the eleventh or twelve segment, into (4) the intestine, which extends to the posterior end of the worm and opens at the anus to the exterior.

During life the first part of the alimentary canal, the "proboscis," is being constantly everted and withdrawn carrying sand or mud, with the contained vegetable and animal organisms, into the oesophagus. During eversion the buccal mass is first extruded, armed with numerous rounded, conical or triangular (Fig. 45, p. 106) vascular papillae; afterwards is everted the pharynx, covered with small rounded processes, which give it a mammillated appearance. In large examples of *A. marina* the pointed tips of the buccal papillae are provided with shining, black or brown, chitinoid caps. There is no other armature associated with the alimentary canal of *Arenicola;* jaws are entirely absent.

The oesophageal glands, which form a valuable diagnostic feature, open into the posterior part of the oesophagus. In *A. pusilla* and *assimilis* there are several of these glandular caeca on each side of the oesophagus (Pl. XIII, Figs. 44, 45); in all the other species only a single pair is present (Pls. IV, IX, VIII, Fig. 17). In *A. marina*, *cristata*, *glacialis* and *loveni* the glands are generally conical in shape, but in some cases, owing to dilatation of their anterior portion, they are clavate. They are usually relatively smaller in *A. cristata* than in other species. In *A. ecaudata* and *branchialis* the oesophageal glands are clavate or flask-shaped, being almost always dilated anteriorly. In the two species, *A. pusilla* and *assimilis*, in which several glands are present, the most anterior caecum on each side is considerably longer than the rest and has usually thinner walls. This anterior gland is generally finger-shaped and may be nearly an inch in length; the others are more or less pear-shaped or ovoid and are much shorter, some of them being only about a millimètre in length.

All the species of *Arenicola* burrow in sand or gravel. Burrowing

is accomplished by repetition of the following operations: the "proboscis" is extended, pressed into the sand, and withdrawn full of sand, which is passed backward into the oesophagus. The body is thrust forwards, partly by the action of the longitudinal muscles and partly by the peristaltic waves produced by the successive contractions of the circular muscles of the body. By the latter means, which causes surging forwards of the coelomic fluid, the anterior end is rendered tense, and, in the caudate species, especially in *A. marina*, becomes dilated, and is thus able to enlarge the depression which has been made in the sand. The passage, which is made partly by the sand being swallowed, partly by its being forced aside, is smoothed by contact with the tense anterior segments, and may be lined with mucus secreted by the epidermis of the anterior region.[1] The first few segments are thus of chief importance in burrowing operations; the branchial region, being in most examples of the caudate species narrower than that which precedes it, is therefore less subject to friction, and in all species the notopodial chaetae are capable, when extended fan-wise, of affording the gills some protection against undue friction. The branchial region of the animal is more or less passively drawn forwards, after each onward thrust of the anterior region, as the animal progresses in its burrow; meantime, the waves of contraction pass regularly forwards from segment to segment, and serve the double purpose of rendering the anterior region turgid and of assisting respiration by agitating the water in the burrow, thus causing a change of water around the gills. These waves are, of course, best seen in the aseptate region of the body. After burrowing more or less vertically downwards, to a depth of from one to two feet, the littoral form of *A. marina* may make a horizontal or oblique passage, and then a second vertical one which opens at the surface of the sand in a small funnel-shaped aperture. This funnel-like aperture is said by M. Bohn to be due to the subsidence of the sand at the surface brought about through the removal of the subjacent sand, during feeding, by the proboscis. M. Bohn believes that from the vertical shaft of the burrow one or more horizontal galleries are formed, but that they have no communication with the exterior. This is undoubtedly sometimes the case, as the writer can corroborate, for, while digging for small specimens about mid-way between tide-marks, he has exposed them in L-shaped burrows. The blind

[1] The sand in contact with the burrow often exhibits a reddish or brownish discolouration, due to some chemical change induced in the iron-containing constituents.

end of the horizontal limb of each of these burrows, where the head of the worm was found, was somewhat dilated. But in most cases, the burrows, when complete, are U-shaped, one end terminating in the funnel and the other being indicated by the casting. The burrows of the Laminarian form of *A. marina* are vertical or L-shaped, and the worms in them are invariably found head downwards.[1] The depth of the burrow of both forms is often such that the anterior region of the worm is situated below the superficial firmer layer of sand, and extends into the subjacent, more or less semi-fluid, mixture of sand and water.

The food and digestion of *Arenicola* have been investigated only in *A. marina*, but no doubt closely similar conditions hold in the other species. The material swallowed consists of sand together with small vegetable organisms, *e.g.* diatoms, small animals and animal remains; occasionally a larger animal is swallowed, *e.g.* Saint-Joseph found in one specimen a partially digested Nereid. This material is passed into the oesophagus, where it is mixed with mucous secretions from the oesophageal cells and, further back, the trypsin-like secretion of the caeca is poured upon it. In the stomach the secretion from mucus-forming and digestive cells is added to the mass. The swinging backwards and forwards of the stomach, brought about by the muscles of the body-wall and by the protrusion and retraction of the proboscis, tends to produce a thorough mixing of the sand and digestive secretions, and thus the latter are brought into contact with the organic substances of various kinds contained in the sand. The soluble products of digestion are absorbed in the sinuses on the stomach by the blood, which passes almost immediately to the hearts, whence it is pumped into the ventral vessel and thus to all parts of the system. The sand or mud, as passed from the intestine by the anus, forms a rounded or trochoid heap of vermicular coils, along each turn of which a thin cord of mucus may often be seen. These coiled castings of *A. marina* are familiar objects on innumerable sandy beaches of northern and western Europe, and similar castings are formed by the other caudate species when feeding in not too coarse a medium.

The burrows of the ecaudate species are oblique or sinuous cavities in the gravel or between the stones and rocks among which these worms live, and the castings, being composed of coarse

[1] Many of the specimens seen in their burrows were found with the anterior and middle parts of the body lying in the horizontal limb, a position doubtless correlated with the greater abundance of water in this region of the burrow.

material, having little coherence, generally soon fall to pieces. In any case the castings are inconspicuous among their surroundings, and therefore do not betray the presence of the worms, as in the case of *A. marina.*

Nervous System and Sense-Organs.

The brain is situated in the prostomium. In the caudate species it may be compared in form to the letter H, or, more accurately, to two slightly flattened pears, lying side by side, with their narrower faces adjacent and fused along the middle third of their length. The more massive anterior portions of the pears represent the anterior, and the tapering portions the posterior brain-lobes, the latter of which lie below the nuchal organ. In the ecaudate species the brain is of simple form—practically non-lobate, almost band-like—and merges at each end into the oesophageal connectives. The brain gives off anteriorly and posteriorly bundles of nerves to the prostomial epithelium and the nuchal organ respectively.

The oesophageal connectives arise, in the caudate species, from the anterior and middle regions of the brain. In all species the connectives run obliquely backwards and ventrally (Pl. XIII, Fig. 46), and unite with the ventral nerve-cord some distance in front of the first chaetiferous annulus—that is, in the achaetous body-segment which precedes the first chaetiferous segment. The course of the connectives and the ventral nerve-cord is indicated externally, in some species, by the metastomial and ventral grooves (Fig. 53, p. 118). The oesophageal connectives give off nerves to those annuli through which they pass, and to the statocysts.

The ventral nerve-cord does not exhibit, in dissections, any obvious signs of segmentation, its nerve-cells are not aggregated into definite ganglia, but are distributed along the lateral and ventral portions of the whole length of the cord. In all species, except *A. pusilla,* there are, at segmental intervals, among the ordinary nerve-cells, much larger "giant cells," which are connected with remarkable "giant fibres." The ventral nerve-cord gives off a pair of nerves to each inter-annular groove, and one or more pairs to each chaetiferous annulus and its parapodia.

The organs of special sense are the statocysts, the nuchal organ (see p. 38), and the eyes. Other sensory structures are the prostomium, the papillae of the "proboscis," scattered sense-cells in the epidermis, the notopodial chaetae (around the bases of which

Prof. Retzius found nerve-endings), and, possibly, the pits present on certain of the chaetiferous annuli of *A. loveni* and *cristata* (p. 35).

The statocysts are the most highly developed sense-organs of *Arenicola*. They are present in all the known species, except *A. pusilla*, and afford valuable help in specific work.

The statocysts of the lugworm were the first statocysts observed in Annelids: they were discovered, in 1838, by Grube, who, however, mistook them for ganglia, but Stannius (1840) and von Siebold (1841) at once recognised the analogy between these organs and the statocysts of Molluscs. Meissner (1857), in a note[1] long overlooked, first showed that the statocysts of the lugworm open to the exterior by means of a canal. During the last twenty years the statocysts of *Arenicola* have been the subject of researches by Profs. Ehlers and Fauvel and Drs. Gamble and Ashworth.

The statocysts are situated a short distance from the brain, external to the dorsal or dorso-lateral portions of the oesophageal connectives (Pl. XIII, Fig. 46). Each statocyst is primarily an invagination of the epidermis, and in *A. marina, assimilis* and *glacialis* the connection with the epidermis and the exterior is maintained by means of a narrow bent tube, the minute aperture of which may be found near the origin of the metastomial groove (see p. 39). The walls of the statocyst and tube are composed of sensory and epithelial cells; some of the latter are glandular and secrete the thin cuticle which lines the vesicle and the tube. Each statocyst contains one or more statoliths, and a fluid composed of a mixture of sea water and the secretions of the gland cells in the wall of the organ.

It is important to note that, in those species in which there is a tube leading from the statocyst to the exterior, the shape and nature of the statoliths vary considerably in different specimens of the same species, according as the tube is functionally open or closed. This has been shown, by the present writer, to be the case in both *A. marina* and *A. assimilis* var. *affinis*. Numerous specimens of the former species, from different localities, have been examined. In those in which the statoliths consist of many foreign bodies, such as quartz-grains, portions of sponge-spicules, frustules of diatoms, etc., practically without any secreted covering (Pl. XIV, Fig. 47), the tube of the statocyst was found to be open; in others in which the original statoliths had become covered with layer upon layer of pale-yellow secreted substance (Fig. 37 A) the tube was found invariably to have

[1] Zeits. ration. Med., 3 Reihe, i. (1857), p. 635 f.n.

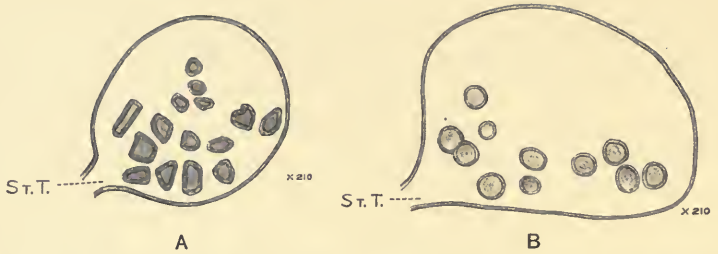

Fig. 37.—*A. marina*. Statoliths, and cuticular lining of statocysts, of specimens from Jersey (A), and Trieste (B). ST.T. Tube leading to exterior.

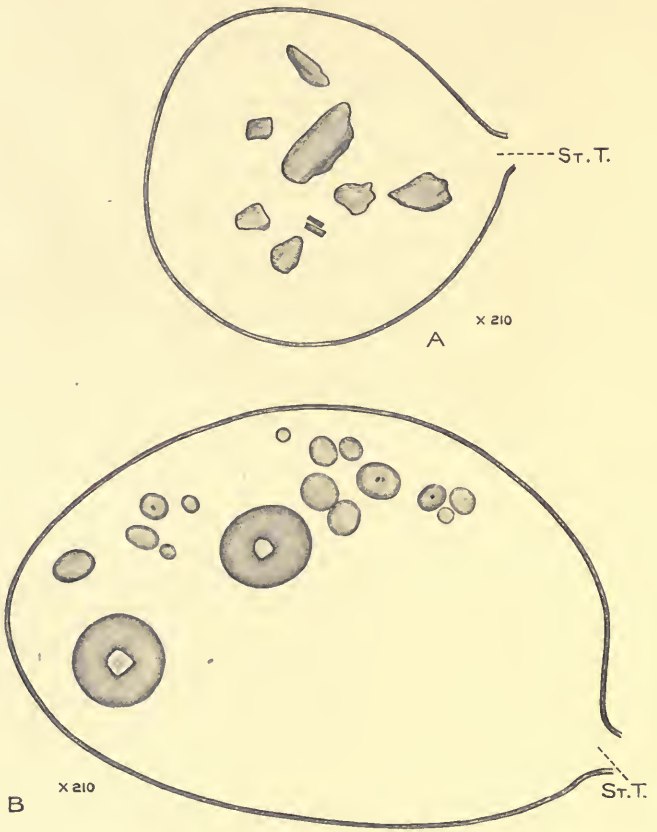

Fig. 38.—*A. assimilis* var. *affinis*. Statoliths, and cuticular lining of statocysts; A, Of a specimen, 136 mm. long, from Otago Harbour, N.Z.; B, Of a specimen, 128 mm. long, from the Falkland Islands. ST.T. Tube leading to exterior,

become closed, either by apposition of its walls or by blocking of its lumen by granular substance secreted by the gland cells in the wall of the tube. A striking instance of this latter condition was exhibited by a specimen from Trieste, in which each statocyst (Fig. 37 B) contained about forty statoliths, approximately spherical, nearly uniform in diameter, and composed almost entirely of secreted chitinoid substance, there being in each only a small central "nucleus." The statocysts were completely shut off from the exterior, the tube of each being closed by a plug of granular secretion.

Similar conditions are met with in *A. assimilis* var. *affinis*. The statoliths of examples from Otago Harbour, New Zealand, are irregular bodies (Fig. 38 A); but those of specimens from near Wellington, New Zealand, from Tasmania and from the Falkland Islands (Fig. 38 B), are rounded, each being composed of a central granule with a thick envelope of yellow secreted material.[1] The canal of the statocyst is moderately widely open throughout its length in the Otago examples, but in all the others is closed at one or more points, generally by small masses of secretion of the same refringent nature as that composing the statoliths. In each statocyst of the two Falkland specimens examined there are two statoliths larger than the rest. They were the first statoliths of the post-larval stage.

These observations on *A. marina* and *A. assimilis* var. *affinis* indicate clearly that the nature of the statoliths depends on whether actual open communication with the exterior is or is not maintained. The form of the statoliths in those species in which a canal leads from the statocyst is variable, and is therefore a character of little value in systematic work.

Only one statocyst of *A. glacialis* is available for examination. The lumen of the tube which connects the statocyst to the exterior is open throughout its length, and the statoliths are numerous naked sand-grains (Fig. 39).

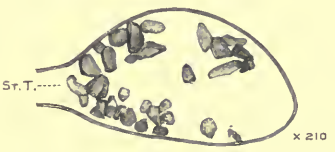

Fig. 39.—*A. glacialis*. Statoliths, and cuticular lining of statocyst. ST.T. Tube leading to exterior.

In *A. cristata*, *loveni*, *branchialis* and *ecaudata* the connection of the statocyst with the epidermis and exterior has been lost, and the organ has become a closed, oval or spherical sac, in which the statolith or statoliths are spherical, oval or lenticular chitinoid bodies. In *A. cristata* (Fig. 40) and *loveni* there is a

[1] The statoliths are of this latter type also in two specimens of *A. assimilis* from Uschuaia.

single statolith throughout life. In *A. ecaudata* and *branchialis* (Fig. 41) there is at first only one statolith. Later many others are formed, but the original one remains conspicuous by reason of its larger size.

The statocysts of *A. assimilis* attain a much larger size than those of any other species: indeed, they are the largest known in the Polychaeta. There is some difference in the size of these organs in similar specimens of the same species from different localities. Fig. 38 A, B, which represent the statocysts of similar specimens of *A. assimilis* var. *affinis*, from Otago and the Falkland Islands respectively, illustrate an extreme instance of local variation in the size of these organs.

The eyes are of simple structure. Each is formed of a lens

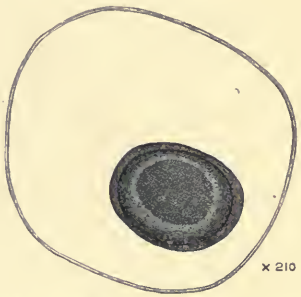

Fig. 40.—*A. cristata.* Statolith, and cuticular lining of statocyst.

Fig. 41.—*A. branchialis.* Statoliths, and cuticular lining of statocyst.

and a cup-shaped mass, about 8 to 20 μ in diameter, composed of reddish-brown pigment-spherules (Pl. X, Fig. 25). In the early stage of larval life the eyes are actively functional, and during the first two days after hatching the larvae are phototropic; but by the third day this preference for light is lost. The eyes soon sink below the epidermis, and become imbedded in the masses of ganglion-cells which form the dorsal and anterior portion of the brain. With the increase in the amount of pigment in the prostomial epithelium the eyes become difficult to find, and are finally indistinguishable. It seems unlikely that in adult specimens the eyes can have any functional importance.[1]

[1] *Arenicola* is sensitive to light, resembling earthworms in its reaction to this stimulus, and, as in them, the response may be due to the stimulation of the sense-cells in the epidermis, especially of the anterior end; it is unlikely that it is due to specific action through the eyes, for the reasons given above.

Nephridia.

There are five pairs of nephridia in *Arenicola pusilla, loveni* and *branchialis,* six pairs in *A. marina, assimilis,*[1] *cristata* and *glacialis,* and thirteen pairs in *A. ecaudata.*

Each nephridium may be divided into three regions—an anterior funnel, a middle excretory portion, and a posterior vesicle or bladder. The funnel, which is usually bright red in colour, owing to its rich vascular supply, opens into the coelom by a slit-like aperture. The larger dorsal lip of the funnel is fringed with ciliated vascular processes, which increase in number and size as the worm grows. In the caudate species these processes are flattened and spatulate or triangular in shape, and their distal margin is usually subdivided into several rounded lobes (Pl. XIV, Figs. 48, 49, 50). In the ecaudate species the processes are more cylindrical, and are more deeply divided distally into two or three, or in large specimens two to six, finger- or thumb-shaped branches (Pl. XV, Fig. 51). The ventral lip is not fringed, and its margin is either entire and almost semicircular in shape, as in *A. marina,* or it is deeply notched in the middle, as in the ecaudate species. In *A. assimilis* the edge of the ventral lip of the funnel is thrown into folds or frills (Fig. 50); a similar condition is very occasionally met with in one or two other species, but in these the "frilling" is much less marked than in *A. assimilis.* In *A. cristata* the middle portion of the ventral lip is often thicker than the rest.

Owing to the reduction in the number of septa in *Arenicola* the typical relationship of nephridium to septum, as exhibited in many Polychaeta and Oligochaeta, is seen in the adult of only three species, and then only in regard to the first pair of nephridia. In *A. marina, assimilis*[2] and *glacialis* the funnels of the first pair of nephridia are situated on the anterior face of the third septum; in the other species the first nephridium is in the following somite.

The excretory part of the nephridium is a thin-walled spacious sac, usually dark brown, sometimes black, in colour, owing to the presence of large numbers of brown excretory granules in the cells lining the sac. This part of the organ tapers posteriorly and leads into the contractile bladder, which opens to the exterior by a small oval aperture situated near, and slightly behind, the dorsal end of the corresponding neuropodium.

[1] South African examples of *A. assimilis* var. *affinis* have only five pairs, the nephridia of the fourth segment being wanting.

[2] Except in South African examples of the var. *affinis* (see footnote [1]).

Reproductive Organs.

The reproductive organs are closely associated with the nephridia. In the caudate species and in *A. branchialis* the gonad is present immediately behind the funnel of each nephridium, except the first, and is a small, ovoid or cylindrical mass of cells (Pl. XIV, Figs. 48–50; Pl. XV, Fig. 51) around the anterior portion or the whole length of the gonadial vessel,[1] which is a continuation of the blood-vessel traversing the dorsal lip of the funnel. The genital products are shed at an early stage from the gonads into the coelomic fluid, and by an examination of this the sex of a given specimen is determinable. There the small groups of spermatogonia undergo repeated division and become successively spermatocytes, spermatids and spermatozoa, large discoidal masses of which are present in the coelom of mature worms. The oöcytes are shed from the ovary when they are about 12 to 20 μ in diameter; while in the coelomic fluid their yolk is elaborated and they grow to the definitive size. The ripe ova of *A. marina*, *pusilla*, *assimilis* and *cristata*[2] are not spherical but biconvex (Fig. 42 B); the face of the ovum is either circular or oval and its two diameters are from ·14 to ·20 mm., while the third axis of the egg is about ·08 mm. The vitelline membrane is comparatively thin, being 1 to 2 μ in thickness. The ova of *A. branchialis* and *ecaudata*, which have a very stout vitelline membrane, 5 to 6 μ in thickness, are oval in shape and are each about ·17 mm. long and ·15 mm. broad (Fig. 42 C).

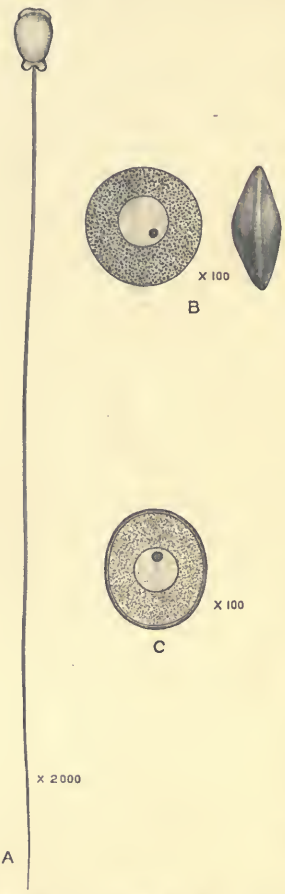

Fig. 42.—A, *A. marina*. Ripe spermatozoon; B, *A. marina*. Ripe ovum, face view by transmitted light, profile view by reflected light: C, *A. branchialis*. Ripe ovum.

The reproductive organs of *A. ecaudata* are much larger and more complex than those of the other species, and form the most striking

[1] There is a gonadial vessel on the first nephridium, but a gonad appears never to be associated with it.

[2] Probably also those of *A. glacialis* and *loveni*, but eggs of these species have not been available in a sufficiently good state of preservation to enable the writer to determine their true shape.

feature in a dissection of this species. In the female the gonad is produced into processes, which at first are few, small, and more or less conical in shape, but later on increase in number and size, and in maturing examples assume very large proportions (Pl. XV, Fig. 52). Such processes are packed with numerous oval oöcytes, about ·12 mm. in diameter, each with a thick vitelline membrane. In male specimens the gonad bears one, two, or occasionally three or four, thin reniform outgrowths, pink, grey or milk-white in colour, according to the condition of their contents (Fig. 53). Within each of these outgrowths, which may attain a length and breadth of 6·0 and 4·5 mm. respectively, are present male cells in all phases of development up to almost ripe spermatozoa. In this species, therefore, the reproductive products are retained in association with the gonad to a much later stage of growth than in the other species of the genus. Just before the breeding period, the envelope of the gonad is ruptured, and the sexual products fall into the coelom and there undergo their final stages of growth.

The genital products, in all the species of *Arenicola*, escape from the coelom to the exterior by way of the nephridia,[1] the vesicles of which are often found, during the breeding season, strongly distended with ova or sperms which have accumulated therein preparatory to discharge.

Development.

Max Schultze [2] found on the island of Neuwerk, off Cuxhaven, large numbers of castings of *Arenicola marina*, and near to many of them a pyriform, greenish-yellow, gelatinous mass, about half an inch in length, fastened into the sand by a gelatinous stem about two inches long. He traced the development of the eggs within these masses, which he regarded as the egg-masses of the lugworm, an opinion shared by a few subsequent writers. Messrs. Cunningham and Ramage and Profs. Ehlers and Fauvel ascribed these egg-masses to *Scoloplos armiger*, and Dr. Groot [3] has definitely proved their parentage by finding them in an aquarium in which specimens of *S. armiger*, but no examples of *Arenicola*, were living.

[1] M. Bohn states that the ova escape by perforations, due to histolysis of the body-wall at the breeding season (C. R. Acad. Sci. Paris, cxxxiii (1901), p. 647). The present writer has not observed this phenomenon in any of the numerous ripe examples which have passed through his hands.

[2] Abh. naturf. Ges. Halle, iii (1856) p. 216.

[3] Proefschr. Univ. Leiden (1907), p. 23.

In spite of the abundance in innumerable places of the adult worm, and of much searching by many workers, the egg-masses of *Arenicola* have never been found on the coast of Europe. The egg-masses of only one species—*A. cristata*—are known, and they have been recorded only from the eastern shore of the United States, from Wood's Holl to South Carolina. They are huge gelatinous masses, often irregularly cylindrical, three to four feet long and two to four inches in diameter, each of which contains several hundred thousand eggs. The vitellus of the egg has a cinnamon colour, so that in bulk the egg-mass has a reddish-brown tint.

The early stages of development of two species of *Arenicola* have been investigated, namely, *A. cristata* by Profs. E. B. Wilson [1] and C. M. Child [2] and Dr. R. S. Lillie,[3] and *A. pusilla* by the writer.[4]

These two species seem to develop along practically identical lines. Within about twenty-four hours after fertilisation, the egg gives rise by spiral cleavage to a blastula, from which a gastrula is formed by growth of the ectoderm cells over the yolk-laden endoderm cells. Shortly afterwards the stomodaeal invagination and the prototroch appear (Pl. X, Fig. 21), and within three days after fertilisation the paratroch is formed, and one or two eyes are present on the anterior portion of the larva (Fig. 22). About the end of the third day the larva pushes its way out of the vitelline membrane through a thin area which had previously made its appearance. During the following day the first pair of notopodial chaetae is formed (Fig. 23), and in the next two or three days the first crotchets are produced. For the first day or two after hatching the larvae are phototropic and swim near the surface of the water; but then they begin to settle down, and may be found crawling about the bottom, surrounded by a more or less tubular film of mucus, with which foreign bodies may be entangled. The belts of cilia decrease in size and soon disappear. The alimentary canal is about this time complete from mouth to anus, and is divisible into three regions—the anterior and moderately active oesophageal part, the stomach, which still contains a considerable amount of yolk, and the intestine (Fig. 24). The coelom, brain and nerve-cord, and muscle-fibres in the body-wall are clearly recognisable. Shortly after the larvae settle down on the bottom, the pharynx becomes active as

[1] Stud. Biol. Lab. Johns Hopkins Univ., ii (1882), p. 278.
[2] Arch. f. Entwick., ix (1900), p. 587.
[3] Mitt. Zool. Stat. Neapel, xvii (1905), p. 341.
[4] Liverpool Mar. Biol. Comm., Mem. xi (1904), p. 55.

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a feeding organ, and food particles are passed into the oesophagus. The subsequent stages of larval development have been followed only in *A. cristata*, to which species, therefore, the succeeding part of this account relates. New segments are formed in the growing zone immediately in front of the anal segment (pygidium) until the full number of chaetiferous segments is attained. Henceforward the segments formed (thirty-eight to forty in number) are of a different nature and are without chaetae (Pl. X, Fig. 30). By the time that about twenty tail-segments have been formed, gills begin to make their appearance on the posterior chaetiferous segments in the manner described on p. 55. The changes which take place in the internal organs have been traced only in relation to the septa, nephridia and alimentary canal. Septa are formed and are for some time present between all the chaetiferous segments, and pro-nephridia are developed in association with the third to the tenth. The first two of these pro-nephridia become degenerate; the others are transformed into the nephridia of the post-larva. In the meantime the regions of the alimentary canal have become more clearly marked; blood, blood-vessels and hearts have been formed, and the nervous system and sense-organs have become more fully differentiated.

Post-Larval Stages, with a Discussion of the Genus *Clymenides*.

Prof. Benham applied the term "post-larval" to that stage of development of *Arenicola marina* in which the worm has attained the full adult number of chaetiferous segments, and is divisible into an anterior chaetiferous region and a posterior achaetous region or tail, but in which the gills are not yet completely formed or have not even made their appearance.

Post-larval stages of five species of *Arenicola* are known, namely, *A. marina, ecaudata, branchialis, assimilis* and *cristata*. Those of the two first-named species have been the subject of considerable discussion, because by some writers they were regarded, not as stages in the growth of *Arenicola*, but as belonging to a separate genus, *Clymenides*.

There can be little doubt that the worm described by Claparède in 1863,[1] and referred by him to a new genus and species—

[1] Beobacht. Anat. wirbell. Thiere Normandie (1863), p. 30, taf. xv, figs. 24–27.

Clymenides sulphurea—of the family Maldanidae,[1] was a post-larval example of *Arenicola marina*. The specimen, which was 3–4 mm. long, was found in mud, surrounded by a mucous tube. There are only two points in which Claparède's account does not fully apply to a post-larval *Arenicola marina*, namely, his specimen is said to have had twenty-two chaetiferous segments, whereas only nineteen are present in *A. marina*, and oesophageal glands are neither mentioned in the description nor shown in the figure (*op. cit.*, Fig. 24) in which the rest of the alimentary canal is represented. Nevertheless the account is so fully in agreement with the characters presented by a young *Arenicola marina* that we may conclude, with Prof. Mesnil, that Claparède was dealing with a post-larval specimen of this species.

Prof. Ehlers[2] described in 1892 the chief features of a young *Arenicola marina*, 3·5 mm. long, enveloped in a gelatinous sheath, taken in the plankton off Heligoland, and of a similar example, taken at the mouth of the Ems, which was examined in sections, and in which the presence of statocysts was ascertained.

A more detailed account of "post-larval" examples of *A. marina* was given by Prof. Benham[3] in 1893. This was based on two specimens, collected near Plymouth, each about 6·8 mm. long, and enveloped in a colourless, transparent sheath.

Prof. Mesnil[4] states that *Clymenides sulfureus* Clap. was taken commonly in the townets at Wimereux in June and July, 1892 and 1893, and that the specimens were evidently similar to those studied by Prof. Benham, and could be described, systematically and anatomically, as young *Arenicola marina*, without gills and with the crotchets of a Clymenid. Although these young worms so closely resembled *A. marina*, Prof. Mesnil preferred to regard them as *Clymenides sulfureus*, and as belonging to the family Clymenidae, a conclusion to which he was impelled largely by the characters of the crotchets.

In his later paper (1897) Prof. Mesnil described two new species of *Clymenides*, namely, *ecaudatus* and *incertus*. Though at first inclined to regard the latter as the young phase of *Branchiomaldane*

[1] Quatrefages (Hist. nat. Annel., ii (1865), p. 249) placed *Clymenides sulfureus* in the family Clymèniens (= Maldanidae); it was included in the Maldanidae also by Prof. Racovitza (Arch. Zool. Expér., sér. 3, iv (1896), p. 229 and f.n.).

[2] Nachr. K. Ges. Wiss. Göttingen (1892), pp. 415, 416.

[3] J. Mar. Biol. Assoc., iii (1893), p. 48, pl. i.

[4] C. R. Soc. Biol. Paris, sér. 10, iii (1896), p. 388; Bull. Sci. France Belg., xxx (1897), p. 144.

vincenti, he concluded, chiefly because of differences in the structure of the chaetae, that the two forms did not stand in this relationship. He believed the genus *Clymenides* (with three species) to be homogeneous, defined it, and regarded it as intermediate between the Clymenidae (Maldanidae) and Arenicolidae. While admitting that he had not seen gonads in any specimen, he expressed the opinion that, if these examples of *Clymenides* had an ulterior development, it would not be towards *Arenicola* but parallel to it. His studies on these worms led him to put forward the view that there is a continuous series connecting the Maldanidae and Arenicolidae, and to suggest the union of these two families (see p. 27).

Prof. Fauvel's[1] investigations led him to the conclusion that *C. sulphureus* was the young of *Arenicola marina*, that *C. ecaudatus* and *C. incertus* were stages in the growth of *A. ecaudata*, and that, therefore, the genus *Clymenides* was invalid. By keeping an example of *C. ecaudatus* in an aquarium until it grew into an *A. ecaudata* 50 mm. long, he produced conclusive proof of the identity of these two forms.

In a paper published in the same year Prof. Mesnil[2] admitted that *C. sulfureus* and *C. ecaudatus* were early phases of *A. marina* and *A. ecaudata* respectively, and expressed the opinion, based on renewed observations, that *C. incertus* was probably the young form of *Branchiomaldane vincenti*. The writer is able to confirm this opinion after having examined, through the courtesy of Prof. Mesnil, the three original specimens of *C. incertus*.

Thus the species of *Clymenides* have been merged either with *Arenicola* or with *Branchiomaldane*, and *Clymenides* therefore disappears as a generic name.

Post-Larval Stages of Arenicola marina.

The earliest known stages of *Arenicola marina* have the full number of chaetiferous segments and about twenty tail-segments. They are found in the surface waters of the sea, not far from shore, each enclosed in a mucous or gelatinous tube, which usually extends beyond the worm at either end (Pl. X, Fig. 26). The worm is capable of wriggling movements, which are but little impeded by the enveloping tube. Nothing is known concerning the duration of the pelagic life of the post-larval stage, but it is apparently at least several days.

[1] C. R. Acad. Sci. Paris, cxxvii (1898), p. 733; Proc. 4th Int. Congr. Zool. (1899), p. 229.

[2] Zool. Anz., xxi (1898), p. 637.

Post-larval stages have been taken off the British, French and German coasts, from March to August, but the majority were found either in March, April, or in the early part of May. Most post-larval specimens of *A. marina* seem to take to a littoral habit before the gills have been formed, or, at any rate, when only a few pairs of gills are indicated: but the writer has two specimens, found free-swimming, which bear the full complement of gills. In one of these the annulation of the body is well marked, and the prostomium is proportionately small; this worm had reached the end of the post-larval stage and would doubtless soon have settled down to its littoral habit.

The following account, based on the examination of about thirty post-larval specimens, some of which were examined alive, applies more particularly to specimens about 4·5 to 6 mm. in length. The prostomium (Pl. X, Fig. 27) is large, conical or spatulate in form, and overhangs the mouth. It bears dorsally, on each side of the middle line, two to four eyes, one of which—that first formed in the larva—is larger than the others. The peristomium is always achaetous. Within it are the statocysts, the internal diameter of which is ·04 to ·06 mm., from each of which the tube leading to the exterior may be traced. The succeeding segment is achaetous in all the specimens examined by the writer, but Profs. Ehlers and Benham found in some of their specimens a minute chaeta in this segment; evidently this is a transitory condition, for the chaeta soon disappears, leaving the segment achaetous, as it is invariably in the adult. Both the peristomium and this segment are generally rather smaller than the succeeding chaetiferous segments, and both are subdivided, usually into two, by a shallow groove, so that, as in the adult, the region between the prostomium and first chaetiferous segment is formed of four rings. The nineteen segments which follow are all chaetiferous, each bearing notopodial and neuropodial chaetae, which are described on pp. 43, 48.

The tail has thirty to fifty segments, of which the anterior are usually the smallest (see p. 38).

The skin is glandular; it contains numerous scattered cells, filled with yellow granules, and mucus-forming cells, which secrete the enveloping tube. The secondary annulation of the skin, which corresponds with that of the adult, is seen in many of these post-larval stages. For an account of the formation of the gills, see p. 55.

The gut, which has already attained the adult form, usually contains only a small amount of food-matter, in fine débris. The blood-vessels and paired contractile hearts are well developed, and

arranged as in the adult, and six pairs of tubular nephridia[1] are present.

Post-larval examples of *A. marina* are from 3·5 to 8·5 mm. long, and may be identified by reference to their general form, their nineteen chaetiferous segments, the presence of six pairs of nephridia (the pores on the fourth to the ninth segments are generally visible), a single pair of oesophageal glands, and open statocysts.

Post-Larval Stages of Arenicola cristata.

Near Beaufort, North Carolina, Prof. E. A. Andrews[2] found, enveloped in a gelatinous tube, a young *Arenicola*, evidently belonging to the species *A. cristata*, in which statocysts were present, each containing a single large statolith. There is no other record of the capture of a post-larva of this species, but Dr. R. S. Lillie has reared specimens in aquaria.

The full number of body-segments, that is, seventeen chaetiferous segments, is acquired by the time the young worm is about 2 mm. in length. When it has attained a length of 5 mm. about twenty tail-segments have also been formed, and gills are beginning to make their appearance on the posterior chaetiferous segments. The worm continues to grow in length, by elongation of the body-segments and by the formation of new tail-segments, until the latter have reached a definite number, namely, thirty-eight to forty (Pl. X, Fig. 30). Meanwhile, the formation of gills proceeds from behind forwards until these organs appear on the seventh segment. The end of the post-larval stage has then been reached, and the worms have become young adults in structure and in form, and are about 6 to 7 mm. long. Most later phases present a tail region comprising considerably fewer than forty segments, due to the readiness with which segments are lost from the posterior end.

The principal diagnostic features of post-larval stages of this species are—seventeen chaetiferous segments, six pairs of nephridia (their pores on the fifth to the tenth segments), one pair of oesophageal glands, a pair of moderately large septal pouches, and a pair of closed statocysts, each containing a single statolith. These characters can be seen in most preserved examples, which have been stained lightly, and cleared carefully in cedar-wood oil.

[1] For an account of their structure, see the writer's Liverpool Mar. Biol. Comm. Memoir (1904), p. 67.

[2] Proc. U.S. Nat. Museum 1891, xiv (1892), p. 300.

Post-Larval Stages of ARENICOLA ASSIMILIS *var.* AFFINIS.

Mr. R. Vallentin found three worms on the surface of the sea, near the Falkland Islands, which the writer[1] has shown to be post-larval stages of *A. assimilis* var. *affinis*. The specimens were 7·6, 8·7 and 11·1 mm long respectively, and were abranchiate. The largest was provided with a transparent gelatinous envelope about 1 mm. in diameter, which covered the worm except for a distance of nearly 1 mm. at each end. These specimens resembled post-larval stages of *A. marina*, except that there were six to eight oesophageal glands on each side (Pl. X, Fig. 29). Six pairs of nephridia were present, and on the last three the gonad was already recognisable. The statocysts were found as two invaginations of the peristomial epidermis, the lips of each being approximated so as to form a short tube. In each statocyst there were four to six statoliths—sand-grains or fragments of spicules. A gill-less post-larval stage of this species and variety, 6·5 mm. long, was found among the "roots" of seaweeds near Uschuaia.[2] These four are the only known post-larval specimens of this species.

Post-larvae of *A. assimilis* may be differentiated from those of all other species of *Arenicola*, except *A. pusilla*,[3] by the presence of several pairs of oesophageal glands. The presence of statocysts, which was established only after careful examination, showed that the specimens described above could not belong to the species *A. pusilla*, but must be examples of *A. assimilis*, and, having nineteen chaetiferous segments, they were referable to the variety *affinis*.

Post-Larval Stages of ARENICOLA ECAUDATA.

The writer has examined about thirty specimens, a dozen of which were abranchiate. The latter range in length from 3 to 9·4 mm., and, in addition to the peristomium and the achaetous body-segment, have fifty-three to fifty-eight fully formed and chaetiferous segments, and two or three recently differentiated and as yet achaetous segments, followed by the pygidium (Pl. XI, Fig. 34). The prostomium is large and bluntly conical, and bears groups of eyes latero-dorsally. The achaetous peristomium contains

[1] Q. J. Micr. Sci., xlvi (1903), p. 764.

[2] Ehlers, E., "Polychaeten," in Hamb. Magalh. Sammelreise, ii, 1 (1897), p. 104.

[3] Post-larval stages of this species have not yet been discovered.

the closed statocysts, each with a single, spherical, secreted statolith. The following segment is achaetous in all the examples seen by the writer, but Profs. Mesnil and Fauvel have recorded the presence, in some of their specimens, of a single capillary chaeta in this segment. The succeeding segments, except in some cases the two or three last formed, are chætiferous. In several of the posterior notopodia there is for a short time a crotchet, accompanied usually by one or more capillary chaetae (p. 40). The characters of the chaetae are described on pp. 40, 43, 53.

Gills are present only in well-grown examples, not less than about 8 mm. long, with approximately sixty fully formed chaetiferous segments. The gills first appear on the sixteenth to eighteenth segments, and then on the succeeding segments (Pl. XI, Fig. 35); but for a considerable time the posterior segments are abranchiate. For instance, specimens with sixty-two and sixty-three segments are gill-less behind the thirty-second and forty-fourth respectively. By the time the gills have become bifid or trifid the worm begins to change its habitat. It leaves the bases of the algae among which it has hitherto lived, and moves to sand or gravel, in which it commences to burrow.

The body-wall is reddish or pale-greenish yellow, or it is dark green, owing to the presence of a considerable amount of pigment, which is especially abundant in the first few segments.

The alimentary canal has assumed the adult form, and the nephridia, of which there are thirteen pairs, are already (in specimens 10 mm. long) becoming saccular, and a definite funnel is present; but the dorsal lip has not yet developed the processes present thereon in the adult.

Post-Larval Stages of Arenicola branchialis.

Among a collection of post-larval and young stages of *Arenicola*, taken in September, 1910, among the "roots" of *Laminaria* in Blacksod Bay (Mayo), by Mr. R. Southern, the writer has found four post-larval examples of *A. branchialis*, the first known specimens. They are 4·4, 5·5, 5·8 and 6·5 mm. long, and have thirty-eight, forty-two, forty and forty-one chaetiferous segments respectively. In the first, third and fourth specimens there are two newly-formed achaetous segments immediately in front of the pygidium. The specimens are abranchiate, and exhibit yellow pigmentation anteriorly and posteriorly.

The general appearance of these worms is similar to that of post-larval *A. ecaudata*, but they have about twenty segments fewer. The chaetae are practically identical with those of *A. ecaudata*, and, as in post-larvae of that species, a crotchet is present in four or five of the last formed notopodia.

Each statocyst contains one large and about eight minute statoliths.

The nephridia, which have simple funnels, are short wide tubes, opening posteriorly on the fifth to the ninth segments. Of great interest is the presence, in one specimen, of paired vestigial funnels in the tenth, eleventh and twelfth segments, suggesting that the series of nephridia probably at one time extended further back than it does now. It is possible that these funnels might have disappeared during the subsequent phases of growth, but they are so well marked, that it seems more probable that the three segments which contain them would have been provided with small funnels, similar to that figured by the writer[1] in the tenth segment of an adult specimen of this species.

Post-larval stages of *A. branchialis* differ from those of *A. ecaudata* in having fewer segments and nephridia.

Examples of *Branchiomaldane vincenti* present a general external similarity to post-larval stages of *A. ecaudata* and *branchialis;* but the former may be recognised by the bi-annulate gill segments, in which the chaetae and gills are on consecutive rings (*cf.* Figs. 33, 35, Pl. XI), by the presence of gonads and only two pairs of nephridia, and by the absence of statocysts and pigment.

Separation of the Genus Arenicola *into Sections and Species.*

The genus *Arenicola* is divisible into two sections, one—the caudate section—contains those species, six in number, which possess a posterior region or "tail" upon which neither parapodia nor gills are borne: the other—the ecaudate section—comprises two species in which the parapodia, and generally also the gills, extend to the posterior end of the worm. In addition to this obvious distinction, the two sections of the genus exhibit several other differential characters, both external and internal.

[1] Q. J. Micr. Sci., xliii (1900), pl. xxvi, fig. 54.

The Caudate Section of the Genus Arenicola.

The characters of the caudate section may be given thus:—The parapodia and gills do not extend to the posterior end of the worm, an achaetous and abranchiate "tail" is present. There are eleven or thirteen pairs of gills, the first borne usually on the seventh [1] or eighth [2] segment; the gills, the axes [3] of which bear branches bilaterally, are either pinnate or fruticose (bushy). The prostomium is trilobate. Each statocyst [4] is either provided with a tube leading to the exterior, in which case numerous statoliths, generally of foreign origin, are present, or it is a closed vesicle containing only a single secreted statolith. The dorsal lip of each nephridium bears a fringe of flattened vascular processes; the margin of the ventral lip is not deeply notched, it may be thrown into folds or frills, but it is more often simple. The gonad is small, the ova are biconvex,[5] and their vitelline membrane thin (1–3 μ).

KEY TO THE CAUDATE SPECIES OF *ARENICOLA*.

1. Nineteen or twenty chaetiferous segments; thirteen (or twelve) pairs of gills, the first on the seventh or eighth segment ..... 2.

   Seventeen chaetiferous segments; eleven pairs of gills, the first on the seventh segment ..... 6.

2. Neuropodia of the posterior branchial segments long, their grooves extending almost to the mid-ventral line; one pair of oesophageal glands; one pair of septal pouches 3.

   Neuropodia of the posterior branchial segments short, forming oval pads on the sides of the segments, their grooves not nearly reaching to the mid-ventral line; several pairs of oesophageal glands; no septal pouches 4.

3. Lobes of the prostomium almost equal in size; nephridia opening on the fourth to the ninth segments; septal pouches small; statocysts each with a tube leading to the exterior, and with numerous statoliths (sand-grains) *marina*, p. 86.

   Median lobe of the prostomium large; nephridia opening on the fifth to the ninth segments; septal pouches *very large;* statocysts closed, each containing a single large secreted statolith ..... *loveni*,[6] p. 103.

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[1] The gill of this segment may be reduced or absent.
[2] In typical examples of *A. assimilis*.
[3] In *A. glacialis* the gill-axes are much reduced and the branches clustered.
[4] Statocysts are not present in *A. pusilla*.
[5] In those species in which ova have been examined in the fresh condition. The ova of two species have not been available in the fresh state.
[6] The notopodial chaetae of this species, with their well developed "Sägeblätter" and transverse striation, are very characteristic (see p. 44).

4. Twenty chaetiferous segments; nephridia opening on the fourth to the ninth segments; statocysts large, each with a tube leading to the exterior and with numerous statoliths ..... *assimilis*, p. 123.

   Nineteen chaetiferous segments ..... 5.

5. Lateral lobes of prostomium of moderate size, not dilated or folded anteriorly; nephridia opening on the fourth (or fifth[1]) to the ninth segments; statocysts present, each with a tube leading to the exterior and with numerous statoliths ..... *assimilis* var. *affinis*, p. 124.

   Lateral lobes of prostomium large or very large, generally folded at their anterior end; nephridia opening on the fifth[2] to the ninth segments; *statocysts absent;* the post-rostral region of the neuropodial crotchets is more dilated and convex than in the preceding species ..... *pusilla*, p. 114. (= *claparedii*).

6. Gills large, pinnate; nephridia opening on the fifth to the tenth segments; septal pouches large; statocysts closed, each containing one large secreted statolith..... *cristata*, p. 105.

   Gills small, bushy; nephridia opening on the fourth to the ninth segments; septal pouches small; statocysts each with tube to the exterior and with numerous statoliths (sand-grains) ..... *glacialis*, p. 111.

It is advisable not to depend on external characters alone when the species *marina, assimilis* and *pusilla* are concerned. An incision should be made along the mid-dorsal line of the specimen, extending from the eleventh segment nearly to the prostomium, so as to permit examination of all the important organs. Especial care is necessary in discriminating *A. pusilla* and *A. assimilis* var. *affinis*. If the prostomial lobes are well preserved they offer most valuable help in diagnosis, but if their preservation is defective reference should be made in turn to the statocysts, crotchets and nephridia. As the statocysts are more or less imbedded in the muscle and connective tissue, careful search is necessary, or they may escape observation.

The Ecaudate Section of the Genus Arenicola.

The characters of the ecaudate section (*Arenicolides* Mesnil[3]) may be stated thus:—The parapodia, and generally also the gills, extend practically to the posterior end of the worm; there is not an elongate "tail," but behind the last chaetiferous annulus there is a terminal conical portion, consisting of not more than about six

[1] In South African specimens of *A. assimilis* var. *affinis*.
[2] Rarely on the fourth to the ninth (see p. 118).
[3] See p. 31.

annuli. Gills are not present on the first eleven or fifteen segments; the main gill-stems, which seem to be of the nature of sympodia, bear branches unilaterally. The prostomium [1] is simple and non-lobate, it is a transverse band or ridge, generally exhibiting a slight median elevation; the prostomium merges into the "upper lip" of the peristomium, and forms with this a conical structure overhanging the mouth. Each statocyst is a closed sac, which contains, in the adult,[2] numerous spherical secreted statoliths. The dorsal lip of each nephridium bears on its margin several digitiform, often bifid or trifid, vascular processes; the ventral lip is deeply notched in the middle. The eggs are oval and have a thick vitelline membrane (5–6 μ).

KEY TO THE ECAUDATE SPECIES.

First gill on the sixteenth segment; thirteen pairs of nephridia opening on the fifth to the seventeenth segments; gonads large..... *ecaudata*, p. 132.

First gill on the twelfth segment; five pairs of nephridia opening on the fifth to the ninth segments; gonads small..... *branchialis*, p. 138 (= *grubii*).

About sixteen other species of *Arenicola* have been founded, but, as will be shown subsequently, they must all be merged with one or other of the eight species mentioned in the keys. Attempts have been made previously, but on insufficient data, to merge some of the species; for instance, Ives (1891) believed that all specimens of *Arenicola* then known could be properly referred to three species, namely, *marina, cristata, ecaudata.* That suggestion was based on imperfect acquaintance with the external, but especially with the internal, characters of several of the species in question. At that time, and for a few years afterwards, the internal anatomy of all the species, except *A. marina,* was practically unknown, and that of two of the species has become known only during the last two years, owing to the investigations carried out by the writer in preparation for this Catalogue.

[1] Prof. Fauvel describes the prostomium of *A. ecaudata* as an obtuse cone, and that of *A. branchialis* as reduced to a simple transverse ridge. The writer has examined a large number of specimens of both species, but cannot find any *constant* difference between them in regard to their prostomia; the variations of form exhibited by the anterior end are due apparently to differences in the amount of contraction taking place on fixation.

[2] In young post-larval stages only a single statolith is present, others are formed subsequently; but the original one is distinguished from the rest by its greater size.

Arenicola marina (Linnaeus).

Plate I; Plate IV, Fig. 10; Plate X, Figs. 26, 27, 28; Plate XII, Figs. 39, 40; Plate XIII, Figs. 43, 46; Plate XIV, Figs. 47, 48.[1]

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[1] For other figures of this species, see Figs. 9, 17, pp. 42, 48, chaetae of post-larval stages; Figs. 13, 18, 19, 20, pp. 46, 49, 50, chaetae of adults; Fig. 31, p. 59, gill; Fig. 37, p. 68, statocysts.

[2] Hill's *L. scaber*, from Bognor (Hist. Anim., iii (1752), p. 15), was probably the lugworm.

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Leach, Encycl. Brit., 4th Edit., Suppl. i (1816), p. 452.

Arénicole des pêcheurs—
Cuvier, Bull. Sci. Soc. Philom. Paris (1802), no. 64, pl. vii, figs. 1–5; Règne Anim., ii (1817), p. 527: *op. cit.*, 2 Édit., iii (1830), p. 197: *op. cit.*, Édit. Disc., Annél. (Edwards), pl. i, pl. viii, fig. 1.

Clymenides sulphurea—
Claparède, Beobacht. Anat. wirbell. Thiere Normand. (1863), p. 30.
Fauvel, Hist. nat. Cotentin, iii (1905), p. 75 (St. Vaast).

Clymenides sulfurea—
Claparède, *op. cit.*, p. 118, Descr., taf. xv, figs. 24–27.

Clymenides sulfureus—
Mesnil, C. R. Soc. Biol. Paris, sér. 10, iii (1896), p. 388 (Wimereux); Bull. Sci. Fr. Belg., xxx (1897), pp. 148, 163.

Eruca marina,[1]—the fishers call it Lug—
Sibbald, Hist. Fife and Kinross (1710), p. 56.

Lugg—
Carew, Survey Cornwall (1602), p. 34 b.

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[1] The "*Eruca marina—ad littus maris in Cornubia*" of Merrett (Pinax Rerum Nat. Brit., Lond. (1667), p. 36), was possibly the lugworm, previously recorded from Cornwall by Carew. Merrett also mentions (p. 196), "*Lumbricus mar.*"

Nereis lumbricoides—
Pallas, Nova Acta Acad. Sci. Imp. Petrop., ii (1788), p. 233, tab. v, figs. 19, 19*.

Orm—
Linnaeus, Skånska Resa (1751), p. 315 (Helsingborg).

Vermis ex arenâ effossus Lug dictus—
Sibbald, Scotia Ill., ii (1684), pars 3, p. 34.

Vermes marini scolopendroides, Cornubiensibus Lugs dicti—
Ray, Hist. Insect. (1710), p. 46.

Ver du Havre—
Dicquemare, Obs. sur la Phys., Rozier, xiii (1779), p. 19, pl. ii.

Caudate *Arenicola* with nineteen [1] chaetiferous segments; thirteen pairs of gills, the first, which is on the seventh segment, may be small or absent; gills either bushy or pinnate; the three lobes of the prostomium are nearly equal in size—at any rate, the lateral lobes are seldom much larger than the median one; neuropodia clearly visible in each segment, in the posterior branchial segments forming long muscular ridges reaching nearly to the mid-ventral line; six pairs of nephridia, which open on the fourth [2] to the ninth segments; one pair of oesophageal glands, conical or club-shaped; one pair of small globular, conical or flask-shaped septal pouches; a pair of statocysts, each with tube to the exterior, statoliths numerous, composed of sand-grains, which may be enveloped to a greater or less extent with material secreted by the walls of the statocyst.

Historical Account.—This worm was first described by Belon (1553), who observed the use of the "proboscis" in burrowing, the power of contraction of the worm, the tufts of hair in the "joints" in front of the plumes [*i.e.* the gills], the yellow colour exuded from it, and the castings.

The first reference to this worm in British literature seems to be that by Carew (1602), which is further noteworthy as being the first record of the name "Lug," [3] by which this species is still commonly known among fishermen.

[1] Prof. Benham (Cambr. Nat. Hist. ii, p. 333) attributes to *A. marina* twenty chaetiferous segments, but this number has been found only in a small percentage of post-larval stages examined; the normal number in young and adult specimens is nineteen.

[2] The first nephridium is not uncommonly reduced or even absent.

[3] Low German—slow, heavy. The word "lob," which is sometimes used instead of lug, is of similar origin, and expresses "the general notion of something heavy, clumsy."

Willughby (in Ray's Hist. Insect.) was the first to enter into detail regarding its external characters, such as the inequality of the rings, the number of "cirri" [notopodia], the presence of a tail and anus. The only internal organs which had been mentioned by previous writers were the "proboscis" and the intestine. Willughby saw the hearts and probably the two series of nephridia, which he called black testes, and the stomach, with its peculiar marking into oval areas, which, however, he mistook for a uterus.

Linnaeus recorded and figured *Lumbricus marinus* in the account of his journey through West Gothland (1747), and introduced the name of this worm into the next (sixth) edition of the "Systema" (1748); but, probably owing to a misprint, the specific name was given as *maximus*. In the tenth and twelfth editions of the "Systema" the worm was named *Lumbricus marinus;* thus Belon's name for the lugworm, which had been in use for two centuries, received the imprimatur of Linnaeus. The generic name has necessarily been changed, and the specific name was, for a time, eclipsed by *piscatorum*, but, being subsequently restored, it remains as a nexus with the earliest mention of this worm in zoological literature.

Dicquemare (1779) published a general description of the external features and colours of the "Ver du Havre," which also included a short account of the gut. He mentioned the extensive use of this worm for bait, and that it was even an object of commerce, being gathered in Basse Normandie and taken to Havre for sale.

Otto Fabricius (1780) gave a clear description of *Lumbricus papillosus*, evidently the common lugworm (see p. 93), in which he referred to the short, foliate, retractile, trifid rostrum [the prostomium], the proboscis, the groove [ventral groove] along the abdomen, the nineteen bundles of setae, protrusible and movable in various directions, and the occurrence behind each bundle, except the first six, of a soft brownish branched cirrus [gill]. The subdivision of the segments into annuli, the presence of a cuticle, the sandy contents of the intestine, the burrows and the spiral castings were also noted.

In 1801 Lamarck founded the genus *Arenicola* for the lugworm (p. 31), but, instead of retaining the specific name which had been so long in use, he re-named it *Arenicola piscatorum*, a designation which was adopted for the lugworm by all subsequent writers, with two exceptions, until 1868. The two exceptions were Templeton

(1836) and Desmarest (1859), both of whom used the name *Arenicola marina*. Malmgren (1868) placed this name at the head of the section dealing with this worm in his well-known "Annulata Polychaeta." Claparède, in immediately following his example, pointed out the incontestable priority of the Linnaean specific name; but the designation *A. piscatorum* had attained such a firm hold that its use was continued for many years after Claparède had shown its invalidity; indeed, it is only during the last ten or fifteen years that the correct name, *A. marina*, has been generally employed.

In 1802 Cuvier, in his paper on worms with red blood, gave an account of the gills and vascular system of *Arenicola*. His figures contain good representations of the hearts and blood-vessels, the gills, setal sacs and muscles, and the alimentary canal. They also show five pairs of "bourses noirâtres" [*i.e.* nephridia], the function of which was unknown to Cuvier, but appeared to him to be connected with reproduction. The function of two other "bourses charnues" [oesophageal glands], attached to the oesophagus, was also then unknown.

Oken (1817) made an unaccountable mistake in the number of gills. He emphasised the statement that there are sixteen pairs, and not fourteen.[1] He gave a good description of the form of the gills and the gut, and pointed out the true nature of the "proboscis."

Savigny (1820) made a more careful examination of the external features of *A. piscatorum* than any of his predecessors. He was the first to notice the presence of crotchets. He also observed, above the first segment, the small trilobed "caroncule" [prostomium], retractile into a transverse groove [nuchal groove].

Milne Edwards gave a short account, illustrated with classical figures, of *Arenicola piscatorum* in Cuvier's Règne Animal. Grube's thesis (1838) contains an excellent description of each system of organs of the worm. Cosmovici (1880) dealt particularly with the circulatory system and excretory organs, and Prof. Ehlers (1892) with the external features of the anterior end, the nervous system, and sense-organs. Vogt and Yung (1888) and Saint-Joseph (1894) have published general accounts of this worm, and Drs. Gamble and Ashworth (1898) a more detailed study of its anatomy and morphology. The memoir of the last-named author (1904) contains the latest description of the lugworm.

[1] O. F. Müller (1806) had stated that the worm had fourteen pairs of gills.

Observations on the Records.—The worms recorded and figured by Olafsen and Povelsen as *Lumbricus littoralis* were specimens of *Arenicola*, and may be safely referred to *A. marina*, which is the only species known from Iceland. *L. papillosus*, first described briefly by Müller, and afterwards in greater detail by Fabricius, was regarded by Quatrefages as a distinct species—*Arenicola papillosa*—because Fabricius had referred to the presence of small appendages at the base of the "rostrum" [prostomium]. The remainder of the description given by Fabricius (see p. 91) accords so accurately with *A. marina*, which is the only species known from Greenland, that there need be no hesitation in referring the record to this species. The appendages, on the presence of which emphasis was laid by Quatrefages, were either the papillae of the upper lip or the everted nuchal epithelium.

Lumbricus punctis prominulis, of the first edition of Linnaeus' Fauna Suecica, was given in the later edition as a synonym of *L. marinus*.

Of the records cited under *Arenicola piscatorum* only a few require comment. Grube (1851) recorded under this name a single specimen collected by Middendorff during his journey "in den äussersten norden und osten Sibiriens." The record is placed here provisionally, for if the specimen was found on the east coast of Siberia it was taken close to the area of distribution of *A. pusilla*, and may have belonged to this species. Grube stated that the specimen was about two inches long, and possessed only eighteen chaetiferous segments and twelve pairs of gills, which numbers are not normal for either *A. marina* or *pusilla*, or indeed for any other known species. The specimen probably belonged to one of these species, but exhibited reduction in the number of segments and gills.

The records by Marcialis from Sardinia, by Marshall from Nice, by Payraudeau from Corsica, and by Vérany from Genoa, should be accepted with caution until other specimens from these localities have been examined and shown to belong to the species *A. marina* and not to *A. pusilla*.

Several of the records of *Arenicola piscatorum* from the Mediterranean and Adriatic almost certainly include *A. pusilla*, which occurs in both seas, and are therefore placed under "*A. piscatorum, partim.*" Grube referred specimens from Italy and Sicily (1838), and from the Mediterranean generally (1840), to the species *A. piscatorum*. In the "Collection Grube" in the Kgl. Zoologisches Museum, Berlin, there is a bottle containing specimens labelled "*Arenicola piscatorum.*

Mittelmeer," possibly some of those mentioned in the two memoirs cited. These specimens belong to the species *A. pusilla* (see the writer's paper on this collection, 1910). Schmarda (1861) stated that he found in the Mediterranean, the Channel and on the coast of the Pacific the same species, *A. piscatorum*; but from a subsequent statement in his description it is clear that the Pacific examples were not of this species.[1] Vogt and Yung mention that the examples of *A. piscatorum* from Naples are smaller than those from the Channel and North Sea. The former are examples of *A. pusilla*. It should be borne in mind, when considering these records, that it was not until 1883 that Dr. Levinsen pointed out the characters which distinguish *A. claparedii* (= *pusilla*) from *A. marina*, and that about fifteen years elapsed before the former species was generally accepted. Up to the time of Dr. Levinsen's memoir all specimens of *Arenicola* with nineteen segments and thirteen pairs of gills had been referred to the species *A. marina*, and this practice prevailed, with only one or two exceptions, until almost the end of last century.

Passing to the records under *Arenicola marina*, the writer has identified, as belonging to this species, specimens in the Kgl. Zoologisches Museum, Berlin, with labels indicating that they were collected in the Marquesas and Kingsmill (Gilbert) Islands; but as the information is regarded as being a little uncertain, the records are stated under reserve. The writer's record from Chile rests upon a specimen, in the collection of the Zoological Institute of Vienna, which Prof. K. Grobben kindly sent for examination. The label reads "*Arenicola piscatorum*, Chile." Although the specimen is not in a good state of preservation, it can be identified with certainty as *A. marina*. There is, unfortunately, no other information as to the history or exact place of capture of the worm. If it be from Chile it is, so far as the writer is aware, the only specimen of *A. marina* from the west coast of America, and before this species is regarded as a constituent of the fauna of that coast it is desirable that other examples be procured therefrom.

Ives referred all specimens of *Arenicola* with six pre-branchial and thirteen branchial segments to "*A. marina*," which was thus made to comprise several species. The localities cited show that, besides *A. marina*, there were included *A. glacialis, pusilla, assimilis* var. *affinis*, and possibly *A. loveni*. The examples placed by Prof. von Marenzeller under "*A. marina*" have been shown by the writer to

[1] For remarks on these specimens, see p. 120.

include representatives of two other species, namely, *A. pusilla* (from Vancouver) and *A. assimilis* var. *affinis* (from Angra Pequeña).

Leach defined *A. carbonaria* as having "body, coal black." The specimen, which was found near Leith, is doubtless that in the British Museum Collection labelled "*Arenicola carbonaria.* Black Rock, Frith of Forth. Mus. Leach." This is a very dark example of *A. marina* (*cf.* Pl. I, Fig. 3).

Ranzani based his species *Arenicola clavatus* on three specimens in the Museum of the University of Bologna.[1] The place of origin of the specimens[2] was unknown. Ranzani distinguished his new species from *A. piscatorum,* as described by Pallas and Cuvier, because the anterior region was inflated and thicker than the middle region, the tail was long and "articulated," and the gills black. The dilatation of the anterior portion, due to the forward rush of the coelomic fluid, and the articulation of the tail, caused by strong contraction of some of the circular muscles, are features of no specific value; they are seen in many specimens of *A. marina* which have been killed quickly in alcohol. The specimen figured by Ranzani was about 217 mm. long, so that, if from the Adriatic or any other European source, it is certain to have been an example of *A. marina,* as the other externally similar European species—*A. pusilla*—attains only about half this length. *A. clavatus* may therefore be safely merged with *A. marina.*

The specimens[3] on which Girard founded the species *A. natalis* were shortly and insufficiently described. Nevertheless, it is certain that they were ordinary examples of *A. marina.* It is evident that Girard mistook the ventral for the dorsal surface, as he stated that the dorsal region was marked by a conspicuous smooth line, dividing on the cephalic region into right and left branches, which united anteriorly. This smooth line, the dorsal position of which was given as one of the specific characters, is, however, mid-ventral: it marks the position of the nerve-cord, and is seen in all specimens of *A. marina.* The other distinguishing features of *A. natalis*—the

[1] During a visit to that Museum the writer made inquiry for Ranzani's specimens, and careful, but unsuccessful, search was made for them; they are no longer preserved.

[2] Oken (Isis (1817), 1452), but without stating his grounds, said that they came from the Adriatic. The writer has examples of *A. marina* from Trieste, which agree closely in size and appearance with those described by Ranzani.

[3] The specimens have apparently not been preserved. The Curator of the Boston Society of Natural History stated, in answer to the writer's inquiries, that he had not been able to locate the type of *A. natalis,* and that there was no record of its having been given to the Society.

cephalic region not club-shaped but tapering, and the reticulation of the anterior end—are worthless as systematic characters, for they depend largely on the degree of extension, and therefore on the mode of preservation adopted. Girard's specimens, which were from Chelsea, Mass., were examples of *A. marina*, which species has been recorded from other stations in the same State.

A. papillosa has been considered already (p. 93). *A. tinctoria* was a light-coloured example of *A. marina*. It was defined by Leach as having "body yellow, inclining to cinereous, beautifully banded with blue; organs of respiration blood-red, tail greenish." There is in the British Museum Collection a specimen labelled "*Arenicola tinctoria*, Musselborough, Frith of Forth. Mus. Leach," probably the type specimen of this species. It is light brown in colour, and in life was probably similar to that represented in Pl. I, Fig. 1, which was also obtained at Musselburgh.

The small worm described and figured by Claparède as *Clymenides sulphurea* or *sulfurea* was almost certainly a post-larval example of *A. marina*, as were also undoubtedly the specimens designated *C. sulfureus* by Prof. Mesnil (pp. 75–77).

Pallas's account and figures of *Nereis lumbricoides*, and his remark on its use as bait for *Gadus* and *Pleuronectes*, show clearly that this worm was *A. marina*. The description given by Linnaeus of the common "Orm" shows that the lugworm was before him, although he attributed to it twenty pairs of bristles.

Bionomics, Varieties, Size.—*Arenicola marina* is abundant in northern and western Europe [1] on numerous beaches, where the sand is not shifting and contains a considerable proportion of the decomposing organic matter on which these worms feed. They are often very numerous near sewage outfalls, and in other places where a rich diet of decomposing matter is available; their absence or comparative fewness in other stretches of sand depends on at least two factors—(1) the purity of the sand, that is, the almost total absence of food; (2) the force of the sea and the constantly shifting character of the sand. *A. marina* is usually present only in small numbers on sandbanks well out to sea, and on certain beaches where decaying matter is scarce; its absence from other beaches is accounted for by the second factors named above. Some idea of the abundance of the worms in favourable situations may be obtained by reference to the enumerations of their castings given on p. 99, and by the

[1] For an account of the distribution, see p. 101.

observation of Dr. Groot, who, working at Helder, dug out in the sand a rectangle, two mètres by one mètre, to a depth of three decimètres, and found in this quantity of sand ninety-three specimens of *A. marina*.

Specimens of *A. marina* may be separated into two kinds or forms—the littoral and the Laminarian—according to their habitat and the nature of their gills. Specimens taken in the littoral zone (pp. 64, 65) are generally found in U-shaped burrows,[1] have bushy gills (p. 58), and average 180 to 230 mm. in length;[2] but occasionally larger specimens, up to 360 mm. in length, are obtained.

Specimens from the upper part of the Laminarian zone, which can be readily obtained only at very low tides, are found in vertical or L-shaped burrows (p. 65), and generally possess pinnate gills (p. 58). Laminarian examples are more massive than those from the littoral zone, and attain a length of 400 mm., and a girth, at the widest part, of about 70 mm. Besides the difference in the character of the gills, noted above, the Laminarian differs usually from the littoral form in the subdivision of the interval between the second and third chaetiferous annuli: in littoral examples this region is almost invariably divided into three rings, while in Laminarian specimens only two rings are indicated. The Laminarian form has been found on the Lancashire coast, in the Firth of Forth, in Salcombe Estuary (S. Devon), in Jersey, on the north-west coast of France, the North Sea coast of Germany,[3] and is represented by two specimens in the British Museum, from Deal.

Beyond the statement by M. Bohn, that *A. marina* leaves its burrow at night to swim in the sea, nothing is known of the habits of this worm when covered by the sea. Prof. Ehlers (1892) has recorded the swimming of adult *A. marina*[4] and the capture, before

[1] Burrows of similar form, occasionally with a heap of sand or mud near one of the apertures, are abundant in Cambrian, and not uncommon in Silurian and Devonian rocks. It is believed they were made by Polychaeta, and some authors attributed them to *Arenicola* (*A. carbonarius* Binney, Mem. Lit. Phil. Soc. Manchester, 2 ser., x (1852), p. 192; *A. didyma* Salter, Q. J. Geol. Soc., Lond., xii (1856), p. 248); but, as the evidence for this was insufficient, the generic name associated with these burrows was changed to *Arenicolites*.

[2] Specimens from near low-water mark are usually larger than those found near high-water mark; those from sand rich in organic matter are larger than those found in purer sand.

[3] This locality is included because the gills of the specimens collected there by Oken are described as being like a mimosa leaf; they must therefore have been markedly pinnate, as is evident also from Oken's figures.

[4] Mr. H. C. Chadwick (19th Ann. Rep. Liverpool Mar. Biol. Comm. (1905), p. 13) observed a specimen make its way slowly upwards, in a large aquarium tank, by strong and frequent flexions of the body.

sunrise, of specimens (80–120 mm. long) in the surface tow-net, in shallow water at Heligoland.

Arenicola marina is present in certain estuaries in which, especially in times of flood, the water is of much less density than sea water. The few records available indicate that *Arenicola* adapts itself less readily than *Nereis* to estuarine conditions—*e.g.* Ferronnière found, while collecting in the estuary of the Loire, that *A. marina* ceased at St. Nazaire—*i.e.* at the mouth of the river, while *N. diversicolor* extended about sixteen kilomètres further up the river, to a point well above Paimbœuf. Similarly only one specimen of *A. marina* was found at Greenlands, three miles up the estuary of the Exe, although *N. diversicolor* was very common there.[1] The water in this estuary is, at certain times, of low density.[2] Recent observations in the Forth show that *A. marina* extends a considerable distance into estuarine water, and, indeed, occurs in situations—*e.g.* a quarter of a mile above Kincardine[3]—which are subject from time to time to submersion in almost fresh water. Above Kincardine the river channel is comparatively narrow; below that town it opens out into the broad estuary. Specimens living above Kincardine will therefore be submerged in water of low density, and, in times of flood, in practically fresh water. Possibly at those times the worms retire deep into the mud, and thus, perhaps, minimise the effects produced by fluctuation in the density of the water.

Food.—*Arenicola marina* feeds on small living organisms, such as diatoms, algae, foraminifera, etc., but probably to a greater extent on the small dead animals—crustacea, worms, etc.—or their fragments, which are to be found in the littoral zone where *Arenicola marina* occurs in greatest abundance. Occasionally a larger object is found in the alimentary tract of the lugworm—for instance, a piece of seaweed, or a partially digested *Nereis*.

[1] J. Mar. Biol. Ass., n.s., vi, pp. 299, 321.

[2] Dr. Michaelsen (*op. cit.* (1896). p. 195) thinks that the decrease in the Polychaete fauna, observed on passing from the Sound and the Belt into the Baltic, is probably correlated with the decrease in the salinity of the water. In the Belt there are ninety-six species of Polychaeta, in the western part of the Baltic only forty-three, and in the eastern part, from and including Rügen, only nine, including *A. marina*. Sassnitz, on Rügen, is the most easterly locality in the Baltic from which *A. marina* has been recorded (Möbius). The occurrence of this worm much further eastwards seems unlikely, for had it been present it would doubtless have been noted in the faunistic lists given for East Prussia. Dr. Alex. Luther, of the University of Helsingfors, has informed the writer that *Arenicola* does not occur in the vicinity of Helsingfors.

[3] The author is indebted to Mr. William Evans for this unpublished record.

The Cleansing of the Sand by the Agency of Arenicola.—The lugworm burrows to a depth of two feet or more,[1] swallowing sand as it goes (p. 64). Some, probably the greater part, of the organic matter in the sand ingested is removed during its passage through the alimentary canal of the worm, and the sand is eventually discharged, in the form of a "casting," on the surface, where it is subjected to further purification by the action of the air and water. This worm performs great service in regard to "the cleansing of the littoral," [2] taking a prominent share in bringing about the removal of substances which, if left to accumulate, would become objectionable. When it is borne in mind how great are the numbers of castings visible on many of our beaches, that they are renewed twice each day as the tide falls, and that probably the worms carry on similar operations during the intervals in which they are covered by the sea, the magnitude of the collective work done by lugworms becomes evident.

Dr. Davison [3] estimated the amount of sand brought to the surface by lugworms on the Holy Island sands. After finding the average number of castings on nineteen measured areas to be 82,423 per acre, he weighed about fifty castings, and from the results calculated that the average amount of sand brought up to the surface each year on these areas was about 1,911 tons per acre, which, if spread evenly, would form a layer about thirteen inches in depth. Taking two feet as the average depth to which the worms descend, the sand in which they live would be passed through their alimentary canal once in every twenty-two months.

The writer (1904) made similar observations near Musselburgh and Portobello, Firth of Forth, on the beaches of both of which lugworms are abundant. In the former locality the castings varied in number from twelve to fifteen per square yard, and were evidently formed by large worms; near Portobello the castings were more numerous—34 to 38 per square yard, but much smaller, so that the amount of sand brought up was about the same in both cases, and was estimated to be about 3,700 tons per acre annually, equivalent to a layer about two feet in thickness.

The Use of Arenicola marina for Bait.—*A. marina* is the best known worm of our shores by reason of its extensive employment

[1] In cold or stormy weather the worms seem to burrow more deeply.
[2] J. Hornell, Journ. Mar. Zool., i (1894), p. 27.
[3] Geol. Mag., n.s., Dec. III, viii (1891), p. 489.

for bait.[1] It forms an excellent bait for flat fish, is also good for Gadidae in general—haddock, cod, whiting,—and is used as a general bait for lines on both sides of the North Atlantic.

Although certain beaches have been regularly despoiled of *Arenicola marina* for use as bait, this worm is still present there in practically undiminished numbers. Prof. M'Intosh suggested that the worms have "resisted the attacks of man because a sufficient stock of ripe examples and the very young are covered at all times by the tide." There are certainly plenty of old examples in the area covered by the tide, judging from the large specimens obtainable at low tide. How far seawards the worms extend it is impossible to say, but no doubt there are very substantial reserves always covered by the sea. Even in the area exposed at an ordinary tide, the number of worms is so great that the removal of those collected at any one gathering of bait makes no appreciable diminution. For instance, the area from which the Musselburgh fishermen dig their bait probably contains at least three millions of the worms, and therefore the removal of a few thousands per day produces little effect on the numbers accessible at ordinary low tides.

Periods of Maturity.—In north-western Europe *A. marina* has two periods of maturity annually, namely, about February to April, and about July to September.

At the conclusion of the larval development, which is unknown, the post-larval stage (described on pp. 77–79), enclosed in a mucous tubular envelope (Pl. X, Fig. 26), becomes for a time pelagic. As a rule the worm settles down to its littoral habitat before gills are formed, but these organs develop almost immediately.

Young specimens, 17 mm. long, from the sand, taken near the end of June, possessed the full number of gills, already well branched; and in every respect, other than the gonads, the worms had assumed the adult form. Probably these worms were produced from eggs laid in the preceding February or March, and were thus about three to four months old at the time of capture. Nothing is known definitely regarding the correlation between the size and age of the subsequent stages of development; specimens five or six inches long are probably about a year old, but no estimate can be given of the age of the large examples obtainable at low spring tides.

[1] The only other Polychaeta at all commonly used as bait in this country are certain Nereids, *e.g. Nereis* (*Alitta*) *virens*. Large quantities of Hermellids are used for bait in the neighbourhood of Marseilles.

Colour.—Young specimens of *Arenicola marina* are almost pink in colour, as the numerous blood-vessels are seen through the translucent body-wall. The gills of such specimens are usually bright red.

Older specimens are darker, but their colour is very variable. The amount of pigment is increased, especially at the anterior end of the worm, which becomes brown or greenish, and in the tail, which becomes yellowish green, while the middle region remains of a pink or light red colour. Some specimens finally become very dark—a velvety greenish black—with beautiful metallic green and iridescent sheen. The gills of these dark examples are generally also pigmented, and thus have a reddish brown or black appearance. The colours of typical light and dark examples are shown in Plate I, Figs. 1 and 3.

The amount of dark pigment present depends to some extent on the age of the specimen, but the nature of the sand in which the worm has been living seems to be a more important factor. It is generally agreed that light coloured examples are found in almost pure sand, while dark ones live in sand or mud containing much organic matter. Light and dark specimens may be taken within a comparatively short distance of each other, in the same beach; but it will generally be found that the dark ones show a predilection for certain places where there is muddy, black sand, or, to state the matter more correctly, the conditions in these areas produce dark worms, while in a neighbouring clean patch of sand the worms are light in colour. The two specimens figured in Plate I were taken at the same time from the beach opposite Fisherrow, Musselburgh.

Distribution.—*Arenicola marina* occurs in suitable situations on the shores of western Europe as far south as Foz de Douro, Portugal. It extends northwards to the extreme north of Norway, and it has been found in the White Sea, off Cape Ragosin in the Kara Sea, and on the west side of Spitzbergen, the last being the most northerly definite locality for the species and genus. *A. marina* is present in the western part only of the Baltic, Rügen being the most easterly locality in which it has been found in that sea. It occurs at Trieste, and possibly at other stations in the western Mediterranean (see p. 93); but its range of distribution in that area has not yet been ascertained. This species is present in the Faeroes, and on the shores of Iceland and Greenland, and extends down the east coast of America as far as Noank, Conn., which is apparently the most

southern limit to the distribution of the species on that coast. There are single records, given, however, under some reserve, from Chile and the Marquesas and Kingsmill Islands (see p. 94).

The distribution, as far as it is known, indicates that *A. marina* is practically restricted to the shores of the North Atlantic Ocean, north of 41° N. lat., the neighbouring parts of the Arctic Ocean and the northern part of the western Mediterranean.

Deal, Kent	R. T. Pritchett, Esq.	95. 4. 30. 1 & 2.
Sandgate	Rev. Geo. Smith.	Old Coll.
Littlehampton	Mus. Leach.	Old Coll.
Plymouth	Norman Coll.	1912. 4. 8. 1 & 2.
,, (post-larval stage)	Ashworth Coll.	1912. 4. 9. 1.
Teignmouth, Devon	Mr. Degen.	86. 9. 23. 1.
Polperro, Cornwall		62. 5. 5. 47.
Penzance, Cornwall	Dr. Baird.	65. 11. 16. 6.
Coast of Cornwall		68. 1. 17. 8.
Jersey		85. 2. 26. 15.
,,	Norman Coll.	98. 5. 6. 20.
Aberystwyth	Mus. Leach.	Old Coll.
,,	,, ,,	,, ,,
,,	,, ,,	,, ,,
Port Erin, Isle of Man	Ashworth Coll.	1912. 4. 9. 18.
Millport, Cumbrae	D. Robertson, Esq.	60. 10. 2. 12.
,, ,,	Ashworth Coll.	1912. 4. 9. 15–17.
Shetland	,, ,,	1912. 4. 9. 6.
("*Arenicola tinctoria*") Musselborough, Frith of Forth.	Mus. Leach.	Old Coll.
Musselburgh	Ashworth Coll.	1912. 4. 9. 2–5.
("*Arenicola carbonaria*") Black Rock, Frith of Forth.	Mus. Leach.	Old Coll.
Berwick Bay	Dr. Johnston.	47. 10. 11. 33.
Holy Is.		Old Coll.
Holy Is.	Dr. Johnston.	Old Coll.
Arcachon, Gironde	Ashworth Coll.	1912. 4. 9. 7. & 8.
Santander	,, ,,	1912. 4. 9. 9.
Trieste	,, ,,	1912. 4. 9. 12.
Klosterelv Fjord, Finmark.	Norman Coll.	1902. 7. 8. 68.
Kola Fjord, Russ. Lapland	Ashworth Coll.	1912. 4. 9. 10 & 11.
Reykjavik, Iceland	,, ,,	1912. 4. 9. 13 & 14.
Godthaab, Greenland	Holboll Coll.	53. 10. 17. 40.
Greenland	Copenhagen Mus.	82. 5. 12. 12.
,,		65. 9. 23. 4.

ARENICOLA LOVENI Kinberg, emend.

Plate III; Plate IV, Fig. 11.

Kinberg, Öfvers. Kongl. Vet.-Akad. Förhandl., 1866 (1867), p. 355 (Port Natal, Durban); Eug. Resa, Zool., vii, Annul. (1910), p. 73, t. xxix, 1.
Ashworth, Arkiv för Zool., vii (1910), no. 5, 1 pl. (Saldanha Bay); Ann. S. Afr. Mus., xi (1911), p. 1, pl. i (False Bay).
Fauvel, Mém. Soc. Nation. Sci. Nat. Math., Cherbourg, xxxi (1899), p. 179.

Caudate[1] *Arenicola* with nineteen chaetiferous segments; thirteen pairs of gills, the first gill on the seventh segment, gills large and pinnate; the median lobe of the prostomium is large, the smaller lateral lobes are of almost uniform width, that is, they are not dilated or lobate at their anterior ends; neuropodia are clearly visible in each segment, those of the branchial and of the two prebranchial segments are long dorso-ventrally and almost reach the mid-ventral line; each notopodial seta bears numerous finely-toothed crests or "Sägeblätter" at regular intervals along the distal third of its shaft, and this part of the seta presents a well-marked transverse striation;[2] five pairs of nephridia, which open on the fifth to the ninth segments; one pair of oesophageal glands; two enormous septal pouches which pass through apertures in the second septum and terminate immediately in front of the third septum; a pair of closed statocysts, each containing a single large secreted statolith.

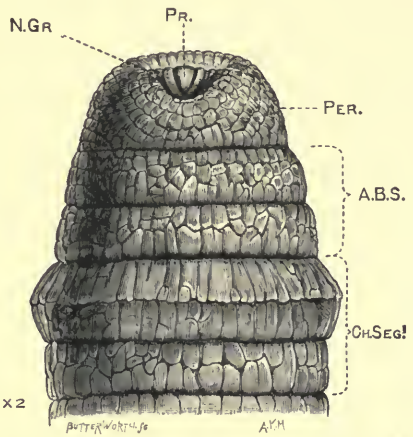

Fig. 43.—*Arenicola loveni*, from Saldanha Bay. Anterior end, dorsal aspect. PR. Prostomium; PER. Peristomium; N.GR. Nuchal groove; A.B.S. Achaetous body-segment; CH.SEG.[1] First chaetiferous segment.

HISTORICAL ACCOUNT.—The species *Arenicola loveni*, which was founded on a specimen collected at Port Natal, near Durban, was defined by Kinberg in the following terms: "Segmentum buccale

[1] Worthy of note is the very large number of tail segments in this species; in three specimens there were respectively 175, 186 and 205 septa in the tail, indicating as many segments.

[2] See Fig. 11, p. 44. Crotchets are shown in Fig. 27, p. 56.

triannulum; segmenta setigera 20 quorum sex anteriora singulumque postremum ebranchiata; longitudo 395–400 mm.; latitudo 20 mm." Following this diagnosis is the reference, "Eug. Resa, Ann., t. xxviii. 1." The plate cited, which forms one of a series containing figures of the Annulata collected on the voyage round the world of the frigate 'Eugenie,' was prepared for issue in 1857, that is, ten years prior to the publication of the diagnosis of the species; but it was not actually published till 1910, though copies were to be found previous to this date in some libraries. In 1910 the original diagnosis was reprinted, and issued with the plate, which was re-numbered xxix.

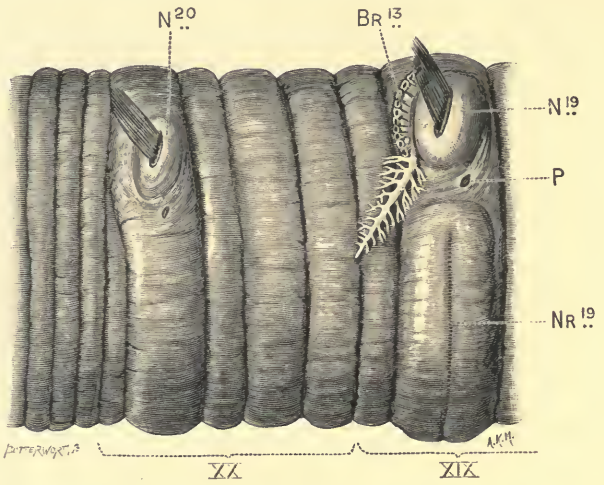

Fig. 44.—*A. loveni.* Type specimen; a portion of the nineteenth chaetiferous segment, the extra (twentieth) segment and notopodium (N 20), and a portion of the tail, seen from the right side. The most ventral axis of the last gill (BR 13) is represented, but only the origins of the other axes are shown; P. Pit (possibly sensory, see p. 35); NR 19, Nineteenth neuropodium.

Prof. Fauvel pointed out that, as far as could be ascertained from the figures on this plate, *A. loveni* differed from a large example of *A. marina* only in the presence of a ring, with a little tuft of chaetae, between the last branchial segment and the tail, and suggested this might be due to error of observation. He concluded that, on the information available, it was impossible to decide whether *A. loveni* should be regarded as a distinct species or merged with *A. marina.*

The writer's examination of the type specimen, placed at his disposal by Prof. Théel, showed that *A. loveni* is a valid species. From the type, and four specimens received from Prof. Gilchrist, and

taken by him in Saldanha Bay, a full description and diagnosis of the species were prepared (1910).

Habitat, Size, Colour.—The habitat of *A. loveni* is similar to that of *A. marina*, the specimens found in Saldanha Bay were a foot or so beneath the surface.

The type specimen is 405 mm. long, the tail being 155 mm. The specimen figured on Pl. III closely approaches the type in length (385 mm.), and in the proportion of body to tail, but is rather stouter.

There are no observations available regarding the colour of this species in life. The appearance of the preserved specimens suggests that, when living, their colour would be similar to that of examples of *A. marina* of light or medium tone.

Remarks on the Type Specimen.—The type specimen possesses an additional chaetiferous, but abranchiate segment, in which, however, only notopodia—smaller than those of the preceding segments—are present (Fig. 44, p. 104). Kinberg's figure [1] and description are correct in regard to this twentieth segment, but, as the type specimen is abnormal in this respect, the diagnosis of the species has been emended so as to state that nineteen chaetiferous segments are present.

Distribution.—*Arenicola loveni* has been found only in three places, namely, Port Natal, near Durban, Saldanha Bay and False Bay, Cape Colony.

Type specimen in Riksmuseum, Stockholm.

Saldanha Bay	Ashworth Coll.	1912. 4. 9. 21.

Arenicola cristata Stimpson.

Plate V, Figs. 12, 13; Plate VIII, Fig. 17; Plate X, Fig. 30; Plate XIII, Figs. 41, 42.[2]

Arenicola cristata—

Stimpson, Proc. Boston Soc. Nat. Hist., v (1856), p. 114 (Maurice I., Charlestown Harb.).

Andrews, Proc. U.S. Nat. Mus. 1891, xiv (1892), pp. 289, 300 (Beaufort, N.C.).

Ashworth, Proc. U.S. Nat. Mus., xxxix (1910), p. 21 (Curaçao; San Pedro and Monterey Bay, Cal.; Suez; Barrow I.; Japan).

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[1] The difference in the sculpturing of the skin of the pre-branchial and branchial regions is not marked and abrupt as shown in Kinberg's figure. Pl. III, Fig. 9, accurately represents the sculpturing of the epidermis.

[2] For other figures of this species, see Figs. 7, 25, pp. 41, 53, chaetae of larva; Figs. 12, 26, pp. 45, 54, chaetae of adult, Fig. 40, p. 70, statocyst.

Arenicola cristata (*continued*)—
Child, Arch. Entw.-mech., ix (1900), p. 587 (Wood's Holl and North Falmouth, Mass.).
Gamble and Ashworth, Q. J. Micr. Sci., xliii (1900), pp. 423, 541, pl. xxii, fig. 1, pl. xxiv, fig. 30 (Jamaica).
Horst, Notes Leyden Mus., xi (1889), p. 40, pl. iii, figs. 6–11 (gills, chaetae).
Ives, Proc. Acad. Nat. Sci. Philad. 1890 (1891), p. 73.
Lillie, Mitt. Zool. Stat. Neapel, xvii (1905), p. 344 (nephr., devel.).
Lo Bianco, Atti R. Accad. Sci. Fis. Mat. Napoli, v, ser. 2, no. 11 (1893), p. 11, tav. i, fig. 1, tav. ii, fig. 1, tav. iii, figs. 5, 6; Mitt. Zool. Stat. Neapel, xiii (1899), p. 484: xix (1909), p. 577.
Verrill, Trans. Conn. Acad. Arts Sci., xi (1901), p. 39: xii (1907), p. 147.
Webster, Bull. U.S. Nat. Mus., no. xxv (1884), p. 323 (Bermuda).
Wilson, Studies Biol. Lab. Johns Hopkins Univ., ii (1882), p. 278 (devel.).

Arenicola ? cristata—
Webster, 32 Ann. Rep. N.Y. State Mus. (1879), p. 117 (New Jersey).

Arenicola antillensis—
Lütken, Vid. Med. Naturh. Foren. Kjöbenhavn 1864 (1865), p. 120 (St. Croix).
Ehlers, Mem. Mus. Comp. Zool. Harvard, xv (1887), p. 173 (Florida; Captiva Key); Zeit. Wiss. Zool., liii, Suppl. (1892), pp. 218, 255, taf. xiii, figs. 30–32.

Arenicola cristata, *partim*—
Fauvel, Mém. Soc. Nation. Sci. Nat. Math. Cherbourg, xxxi (1899), p. 169.
Mesnil, Bull. Sci. France Belg., xxx (1897), p. 163.

Caudate *Arenicola* with seventeen chaetiferous segments; eleven pairs of gills, the first situated on the seventh segment; gills large

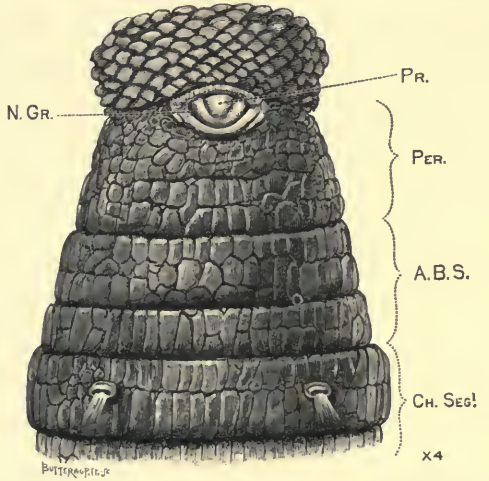

Fig. 45.—*A. cristata*, from Wood's Holl. Anterior end, dorsal aspect; buccal mass protruded: PR. Prostomium; PER. Peristomium; N.GR. Nuchal groove; A.B.S. Achaetous body-segment; CH.SEG!. First chactiferous segment.

and pinnate, their axes generally joined basally by a web-like membrane; median lobe of the prostomium larger than the lateral lobes;

neuropodia are absent on the first and usually also on the second and third segments; the neuropodia of the posterior branchial region are long dorso-ventrally and almost reach the mid-ventral line; six pairs of nephridia, which open on the fifth to the tenth segments; one pair of oesophageal glands, conical, cylindrical or clavate, and comparatively short; a pair of large finger-shaped septal pouches; a pair of closed statocysts, each containing a single, large, secreted statolith.

Historical Account.—This species was founded by Stimpson to contain some large examples of *Arenicola* collected by him on the shore of Maurice Island, at the entrance to Charlestown Harbour. He noted that in these specimens there were only seventeen chaetiferous segments and eleven pairs of highly contractile gills, each composed of twenty main axes bearing regularly arranged branches, and that, on the tail region there were thick cutaneous processes. He also recorded observations on the colours of the living animals, and on the nature of their burrows and egg-masses. Stimpson's description was apparently not known to Lütken, who re-described in accurate detail the external features of this species, under the name of *A. antillensis*. Lütken drew special attention to the strikingly pinnate character of the gills, which he believed to be so important as to require the formation of a new sub-genus—*Pteroscolex*—for the reception of this species. As is shown on p. 31 this sub-genus could not be upheld, and has not been accepted by subsequent workers.

The first record of, and observations on, examples of *A. cristata* from the Old World were those of Dr. Horst, who gave an account of the gills and chaetae of Neapolitan specimens. Prof. Ehlers studied the anterior end and statocyst, and Lo Bianco described the external features and habitat of Neapolitan examples; his Tav. I, Fig. 1, gives a good idea of the colouration of the body, but the gills, which are represented as being brownish, are usually a rich dark red colour.

Prof. Fauvel and Drs. Gamble and Ashworth gave accounts of the anatomy; and the admirable researches, first of Prof. E. B. Wilson, and subsequently of Prof. Child and Dr. R. S. Lillie, have made known the course of development of this species from the egg-cleavage to the adult.

Observations on the Records.—There is no doubt that Stimpson's *A. cristata* and Lütken's *A. antillensis* are the same species.

Stimpson's type is apparently no longer in existence,[1] but Lütken's specimens are preserved in the Universitetets Zoologiske Museum, Copenhagen, and were recently examined by the writer, who found them to agree in every respect with examples from Florida, Carolina and Massachusetts.

Profs. Mesnil and Fauvel included in this species *A. glacialis*, which, at the time of publication of their memoirs, was insufficiently described, but the writer has shown that *A. cristata* and *glacialis* are distinct species.

Bionomics.—Like other species of *Arenicola*, *A. cristata* seems to be more abundant in sand containing a considerable proportion of decomposing organic matter (Lo Bianco, 1899; Lillie, 1905). Mr. Cyril Crossland found specimens near Suez in clean sand, but this was rich in Foraminifera, which no doubt served as food for the worms.

A. cristata descends in the sand or mud to a depth of twelve to eighteen inches, or, in some cases, two feet. The burrow, in which the worm is found head downwards, is, according to Stimpson, at first vertical and then almost horizontal, and thus resembles that usually made by a Laminarian example of *A. marina*. The entrances to the burrows of the massive American specimens of *A. cristata* are large and conspicuous.

Mr. Crossland has informed the writer that the burrows of *A. cristata*, which he saw at Suez, were very deep and U-shaped, and, like those of littoral examples of *A. marina*, their two ends were marked respectively by a heap of castings and a funnel-shaped depression.

Size.—This is the largest species of the genus. Stimpson saw one or more specimens sixteen inches (400 mm.) long and an inch in diameter. The writer has had six specimens from Wood's Holl, each exceeding 400 mm. in length; one of them was a veritable giant among Polychaeta, as it had attained a length of 515 mm. (the tail was 190 mm. long) and a girth of 75 mm. Specimens almost as large have been received from Florida and North Carolina. Most American examples, though large, are, however, considerably shorter

[1] The Curator of the Boston Society of Natural History, to whom I wrote for information regarding the type specimen, kindly informs me that it is not in the Society's Museum, but that it was probably in Stimpson's own collection, and, if so, was in all likelihood destroyed with the Chicago Academy of Sciences in the great Chicago fire.

than those mentioned above; they usually range in length from about 200 mm. to 300 mm. (tail about 60 to 100 mm.).

The Neapolitan are more slender than the American specimens, especially in the tail region (*cf.* Figs. 12, 13, Pl. V). The former are stated by Lo Bianco (1893) to attain a length of 400 mm.; ten specimens seen by the writer were from 200 to 300 mm. long. The examples from Suez were smaller, namely, 120 to 185 mm. in length.

Colour.—In life *A. cristata* displays beautiful colouration. In Neapolitan specimens the greater part of the body generally exhibits a fine dark green colour, with play of iridescence; sometimes the middle region is brown. The gills are almost invariably of a rich dark red or deep crimson colour, and the notopodial chaetae golden yellow. American and West Indian examples seem to exhibit similar colouration, according to the accounts of Stimpson, Verrill and others. Mr. Crossland found, among the examples collected at Suez, two of a deep greenish-black colour, and others were yellowish or pinkish.

Variations in the Organs.—The first gill is subject to considerable variation in size, but it is rarely wanting. In one specimen a very small additional gill is present, namely, on the left side of the *sixth* segment; this is the only specimen of *Arenicola*, out of some thousands seen by the writer, in which a gill occurs in front of the seventh segment.

In American examples of this species the tail usually consists of few segments, about seven to ten;[1] each specimen, when adult, has therefore about thirty caudal segments fewer than it had in the post-larval stage, due to loss of segments from the posterior end. Each tail-segment consists of a large annulus and a number of smaller ones; the former bears a series of hollow thumb-shaped processes, which are generally largest in the first caudal segment, where they attain a length of about 2 mm. Occasionally the most dorsal one is branched distally and resembles a small gill (Pl. V, Fig. 13). The morphology of these processes is obscure; it has been suggested that they are rudimentary gills, and the position and branching of the dorsal member of the series lends some support to this view, but there is no evidence that the more ventrally placed outgrowths are more than exaggerated epidermal papillae. There is some variation in the degree of development of the processes, even in specimens from neighbouring localities; but, as a rule, they are well developed

[1] One specimen has seventeen tail segments.

in examples from the east coast of the southern United States and from the West Indies and Bermudas; they are smaller in Californian specimens.

Neapolitan specimens generally exhibit a considerable number of tail segments: as many as forty may be present (Pl. V, Fig. 12). The epidermis of the tail is raised into numerous papillae, but they are all of the same type; slightly larger ones are present on the larger segmental rings, but there are no thumb-shaped outgrowths such as occur in the American examples described above. The specimens from Suez, Barrow Island and Japan agree with those from Naples in lacking special caudal processes.

The number of nephridia is practically constant in this species. Two interesting departures from the normal number have, however, been found: one specimen possessed an additional nephridium on one side, and another had an additional pair, in both cases in the segment following that normally bearing the last nephridia.

Period of Maturity, Development.—Stimpson and Andrews found the egg-masses of *A. cristata* about the burrows, on the shores of Carolina, during the latter part of March. The breeding season of this species at Wood's Holl extends from May to August, and is at its height in the middle of June. Lo Bianco states that Neapolitan examples are mature from June to August.

This is the only species of *Arenicola* of which the egg-masses are known, and they have been found only on the eastern coast of the United States, at and south of Wood's Holl. They occur in the form of gelatinous ropes, three to four feet long and two to four inches in diameter, each containing several hundred thousand eggs.[1] The masses are at first associated with the burrows of the worms, but, as they are swayed about by the tide, they are liable to be washed loose. Accounts of the development and of post-larval stages are given on pp. 74, 75 and 79.

Distribution.—*Arenicola cristata* has been found on the east coast of the United States, from Wood's Holl, Mass. southwards, at a number of stations, and seems to be quite common in some places. Prof. Andrews states that he found it to be "abundant" and "excessively numerous" in two localities near Beaufort, N.C. It extends along the western coast of Florida to Pensacola, which is the most westerly point in the Gulf of Mexico from which the species has been obtained. *A. cristata* occurs also on several of the

[1] 300,000, according to an estimate by Prof. Andrews.

Floridan Keys, in the West Indian Islands, *e.g.* Jamaica and Santa Cruz, and in the Bermudas. It was reported by the writer from Curaçao, this being the first record from South America.

A. cristata has been known for more than twenty years from Naples, but has not been recorded from any other station in the Mediterranean. It was never common at Naples, and latterly seems to have become more rare.

This species is evidently widely distributed in the Indo-Pacific Ocean, but it has, as yet, been found only at a few stations. Mr. Crossland obtained it in the mud flats near Suez, and the writer has recorded specimens from Barrow Island (north-west Australia), from Misaki and Tomo Harbour, Japan, and from San Pedro and Monterey Bay, California.

The range of distribution may be stated thus:—*A. cristata* is known from Naples, Suez, the warmer parts of the Indo-Pacific Ocean (records from north-west Australia, south Japan and California), the Atlantic sea-board of the United States from Wood's Holl southwards, the Bermudas, and the eastern parts of the Gulf of Mexico and the Caribbean Sea (including the West Indies).

All the stations at which specimens have been obtained are in latitudes less than 40°, except Naples and Wood's Holl, which, however, are very little north of this parallel. *A. cristata* appears therefore to occur only in the tropics or on the shores of the warmer temperate regions; its distribution thus presents a sharp contrast to that of the northern *A. marina* and the austral *A. assimilis*.

Naples	Norman Coll.	98. 5. 6. 1 & 2.
Suez	Ashworth Coll.	1912. 4. 9. 22.
Wood's Holl	,, ,,	1912. 4. 9. 23.
,, ,, (larvae) . . .	,, ,,	1912. 4. 9. 24.
,. ,, (post-larval stages) .	,, ,,	1912. 4. 9. 25.
Florida	,, ,,	1912. 4. 9. 26.

Arenicola glacialis Murdoch.

Plate VI.[1]

Arenicola glacialis—

Murdoch, Rep. Internat. Polar Exped. to Point Barrow, Alaska (1885), p. 155; Proc. U.S. Nat. Mus. 1884, vii (1885), p. 522.

Ashworth, Proc. U.S. Nat. Mus., xxxix (1910), p. 24.

Caudate *Arenicola* with seventeen chaetiferous segments; eleven pairs of small gills, the first situated on the seventh segment; the gill-axes are very short and bear at their distal ends few branches, each

[1] For other figures of this species, see Fig. 23, p. 52, crotchets; Figs. 33, 34, p. 60, gills; Fig. 39, p. 69, statocyst.

of which is either simple or divides dichotomously once or twice, the finger- or thumb-shaped gill-filaments forming clusters at the end of each axis; the median lobe of the prostomium is small, the lateral ones are well developed but not markedly dilated and not folded at their anterior ends; neuropodia are clearly visible in each chaetiferous segment, those of the posterior branchial segments are long dorso-ventrally and almost reach the mid-ventral line; six pairs of nephridia, which open on the fourth to the ninth segments; one pair of conical oesophageal glands; a pair of small septal pouches; a pair of statocysts, opening to the exterior, and each containing numerous statoliths composed of sand grains.

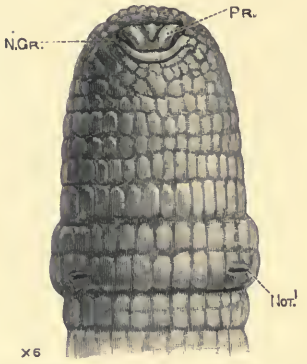

Fig. 46.—*A. glacialis*. Anterior end, dorsal aspect; PR. Prostomium; N.GR. Nuchal groove, the posterior lip of which is slightly everted. Both the first notopodia (NOT.1) are retracted, leaving slits on the surface of the segment.

HISTORICAL ACCOUNT.—A few specimens of *Arenicola*—five picked up on the beach (12th Sept., 1882) at Cape Smyth, Alaska, after a fresh westerly gale, and two mutilated ones taken from the gullet of an eider duck—provided the material on which this species was based. Murdoch gave little information concerning his new species; he remarked that the worms under observation were closely allied to *A. marina*, but they had only eleven branchiferous segments. He described a gill as consisting of a cluster of about fifteen simple cirri, and noted that the tail, which formed about one-third of the total length of each worm, was without tubercles or other appendages. Murdoch gave no figures and no other information regarding his species, which was therefore defined insufficiently. Prof. von Marenzeller (1888)[1] held that, according to the characters mentioned by the author, this species was not separable from *A. marina*, a view shared by Saint Joseph (1894)[2] and Prof. Ehlers (1901)[3]; but Profs. Mesnil (1897) and Fauvel (1899) considered *A. glacialis* as a synonym of *A. cristata*.[4]

[1] Zool. Jahrb. Abt. Syst., iii (1888), p. 15.
[2] Ann. Sci. Nat. Zool., sér. 7, xvii (1894), p. 123.
[3] Fests. K. Ges. Wiss. Göttingen (1901), p. 176.
[4] References to these two papers are given in the synonymy of *A. cristata* (p. 106).

The original specimens were sent recently to the writer, who has shown that *A. glacialis* is a distinct species, and has given the first description of its more important features.

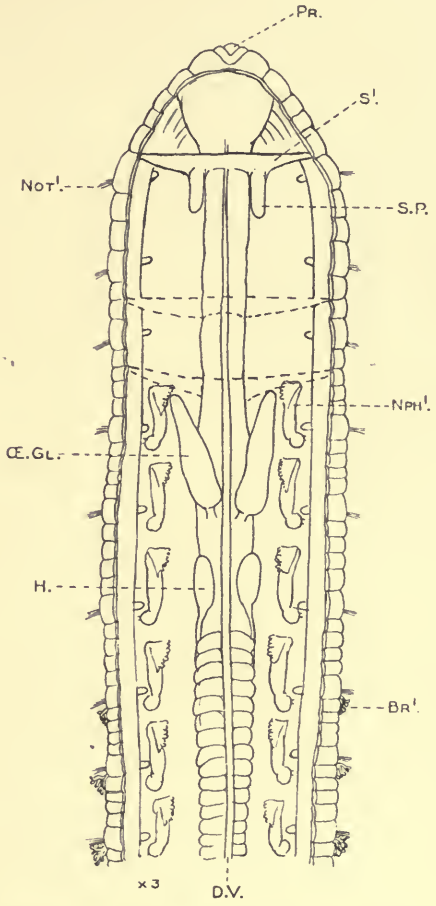

Fig. 47.—*A. glacialis.* Diagram of a dissection of the anterior portion. BR¹. First gill; D.V. Dorsal blood-vessel; H. Heart; NOT¹. First notopodium; NPH¹. First nephridium; (Œ.GL. Œsophageal gland; PR. Prostomium; S¹. First septum; S.P. Septal pouch.

REMARKS ON THE TYPE SPECIMENS.—Of the five original examples only one is complete, another is in two parts held together by a strand of muscle, the other three are in pieces. All are dark brown or nearly black in colour. The complete specimen, shown

in Pl. VI, Fig. 14, is 90 mm. long; the tail is strongly contracted, being only 11 mm. in length. In the figure the tail has been represented in a rather more normal condition of extension. This specimen possesses on each side a neuropodium additional to the number normal for the species. The second specimen is 105 mm. long, the tail being 45 mm. in length.

The striking feature of the specimens is the small size of the gills, the longest axes of which are not more than 2 mm. from their origins to the tip of their terminal filaments (p. 60). The clusters of filaments at the ends of the very short axes, together with the number of the gills, are characteristic of the species. In the only other species in which there are eleven pairs of gills, namely, *A. cristata*, these organs are highly developed and pinnate, and are in complete contrast to those of *A. glacialis*.

Murdoch states that the branchial segments have six rings, but the writer found in every case only five.

The papillae on the tail are very feebly developed; there are no processes present such as occur on the tail of American examples of *A. cristata*.

The crotchets are similar to those of *A. marina* (p. 51).

The diagram on p. 113 embodies all that could be ascertained about the internal anatomy of the only fragment it was permissible to use for inspection of the organs. The small septal pouches, the single pair of oesophageal glands, and the nephridia, are similar to those of *A. marina*. The statocyst is small; its interior is shown in the section figured (Fig. 39, p. 69), which indicates the origin of the tube leading to the exterior.

Types, the only specimens known, in the Smithsonian Institution, Washington.

Arenicola pusilla Quatrefages.

(*A. claparedii* Levinsen.)

Plate VII, Fig. 15; Plate VIII, Fig. 18; Plate X, Figs. 21–25; Plate XIII, Fig. 44; Plate XIV, Fig. 49.[1]

Arenicola pusilla—
Quatrefages, Hist. nat. Annel., ii, p. 266 (Coquimbo).
Ashworth, Ann. Sci. Nat. Zool., sér. 9, x (1910), p. 115.
Fauvel, Mém. Soc. Nation. Sci. Nat. Math. Cherbourg, xxxi (1899), p. 176.

[1] For other figures of this species, see Fig. 8, p. 41, chaetae of larva; Figs. 15, 24, pp. 47, 53, chaetae of adult; Fig. 32, p. 59, gill.

Arenicola claparedi [*sic*]—
Levinsen, Vid. Med. Naturh. Foren. Kjöbenhavn (1883), p. 134 (Naples).
Horst, Notes Leyden Mus., xi (1889), p. 38, pl. iii, fig. 1 (gills, chaetae).

Arenicola claparedii—
Ashworth, Q. J. Micr. Sci., xlvi (1903), p. 773; Mitt. Zool. Mus. Berlin, iv (1910), p. 349 (Ossero; No. Japan); Proc. U.S. Nat. Mus., xxxix (1910), p. 11 (Aleutian Is.; Vancouver; Humboldt Bay, Cal.).
Ehlers, Zeits. Wiss. Zool., liii, Suppl. (1892), p. 246, taf. xiii, figs. 21–29.
Fauvel, *tom. cit.* (1899), p. 175.
Gamble and Ashworth, Q. J. Micr. Sci., xliii (1900), p. 423, *etc.*, pl. xxiv, figs. 26–29 (Crescent City, Cal.).
Lo Bianco, Atti R. Accad. Sci. Fis. Mat. Napoli, v, ser. 2, no. 11 (1893), p. 9, tav. ii, fig. 3; Mitt. Zool. Stat. Neapel, xiii (1899), p. 484: xix (1909), p. 576.

Arenicola claparedei [*sic*]—
Johnson, Proc. Boston Soc. Nat. Hist., xxix (1901), p. 421.

Arenicola marina—
Child, Trans. N.Y. Acad. Sci., xvi (1898), p. 387 (Puget Sd.).
Claparède, Annél. de Naples (1868), p. 300.
? *Ehlers*, Fests. K. Ges. Wiss. Göttingen (1901), p. 176 (Puerto Montt, Chile).
Jaquet, Mitt. Zool. Stat. Neapel, vi (1886), p, 347, taf. xxi, figs. 50, 51, 57, 58.
Lo Bianco, Mitt. Zool. Stat. Neapel, viii (1888), p. 401.

Arenicola marina, *partim*—
Ives, Proc. Acad. Nat. Sci. Philad. 1890 (1891), p. 74.
Marenzeller, Zool. Jahrb. Abt. Syst., iii (1888), p. 12.

Arenicola piscatorum—
Grube, Insel Lussin u. Meeresfauna (1864), p. 87, (Ossero); ? Vid. Med. Naturh. Foren. Kjöbenhavn 1858, (1859), p. 120 (Callao).

Arenicola piscatorum, *partim*—
? *Delle Chiaje*,[1] Descr. Anim. invert., iii (1841), p. 92; v, p. 100.
Grube, Anat. Phys. Kiemenw. (1838), p. 1; Act. Ech. u. Wurmer d. Adriat. (1840), p. 66.
? *Schmarda*, Neue wirbell. Th., i (1861), 1te Hälf., p. xvii: 2te Hälf., p. 52.

Arenicola assimilis, *partim*—
Ehlers, Polych., in Hamb. Mag. Sammelreise, ii, 1 (1897), p. 104 (California).

? **Lumbricus marinus**, *partim*—
Delle Chiaje, Mem. Anim. s. Vert., ii (1825), p. 423.

? **Chorizobranchus marinus**—
Quatrefages, Hist. nat. Annel., ii, p. 267.

Caudate *Arenicola* with nineteen chaetiferous segments; thirteen pairs of gills, the first, which is on the seventh segment, may be small or absent; gills usually of the pinnate type, but occasionally bushy; lateral lobes of the prostomium much larger than the median lobe, and generally folded in their anterior portion; neuropodia

[1] For comments on this record, see p. 144.

clearly visible in each segment, those of the posterior branchial region are short and do not approach the mid-ventral line; the distal part of each crotchet has a form resembling that of a swan's head, that is, the region just proximal to the rostrum of the crotchet has

Fig. 48.—*A. pusilla*, from California. Anterior end, dorsal aspect; showing the large and folded lateral lobes of the prostomium.

Fig. 49.—*A. pusilla*, from Atka Island. Anterior aspect, showing the prostomium (PR.), with its large lateral lobes, the nuchal groove (N.GR.), and the mouth (MO.).

a full, convex curvature,[1] and is proportionally larger than in any other species; five pairs of nephridia, which open on the fifth [2] to the ninth segments; several (four to sixteen) pairs of oesophageal glands, the anterior fairly long and slender, the others shorter and more or less pear-shaped; septal pouches absent; *statocysts absent.*

Historical Account and Remarks on the Type Specimen.—The species *Arenicola pusilla* was founded by Quatrefages on a single incomplete specimen from Coquimbo, Chile. The diagnosis—"Annuli ebranchiati 9. Branchiae magnae ramosissimae"—the only information given, was inadequate, and the position of this with regard to other species of the genus was indeterminable until the writer (1910) examined the type specimen.

Claparède (p. 301) seems to have suspected that Neapolitan examples of "*A. marina*" might be specifically distinct from North Sea specimens. He noted that the former were much smaller and that their gills were not bushy; but it is remarkable that, while studying the blood-vessels and nephridia, he did not observe and

[1] This character is especially clear in specimens not more than about 100 mm. in length.

[2] Rarely is a nephridium present opening on the fourth segment.

comment upon the presence of several oesophageal glands. Dr. Levinsen placed the Neapolitan specimens in a new species, "*A. Claparèdi*," distinguished from *A. marina* by the presence of pinnate gills and by certain chaetal characters,[1] which, however, are valueless for specific discrimination. As pinnate gills occur in some specimens of *A. marina* this character does not serve to differentiate Dr. Levinsen's species. Under these circumstances it is not surprising that many years elapsed before this species was accepted generally. It was, in fact, not until examination had shown that the internal organs depart very markedly from those of *A. marina* that Dr. Levinsen's species could be regarded as definitely established.

Dr. Horst made a careful study of the gills and chaetae; Prof. Ehlers described the external features of the anterior end, and demonstrated the absence of statocysts[2]—the most remarkable character of this species; Prof. Fauvel gave a general description of the internal organs, and Drs. Gamble and Ashworth a more detailed account of the species, recording the first extra-Neapolitan specimen.

The writer (1910) has made an exhaustive examination of the type specimen of *A. pusilla*, which is about 35 mm. long and 3 mm. in diameter, and is incomplete, only the anterior region, as far back as the eleventh chaetiferous segment, being preserved. The first gill is borne on the eighth segment, not on the tenth as stated by Quatrefages, but is small. The neuropodia of the branchial region are of the short type, and the crotchets (Fig. 24 B, p. 53) present distally the form of a swan's head, previously found to be characteristic of *A. claparedii*. The prostomium (Figs. 51, 52, p. 118) is very fully extended, bringing into view the posterior median portion, which in most specimens is hidden in the

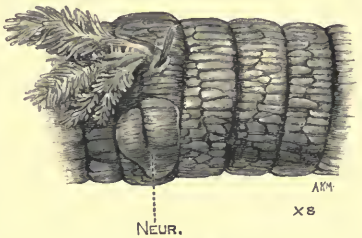

Fig. 50.—*A. pusilla*. Type specimen, right aspect of the tenth chaetiferous segment. Note the short, wide neuropodium (NEUR.).

[1] The footnote, which gives Dr. Levinsen's diagnosis of the species, is as follows: "Den middelhavske Art, for hvilken jeg foreslaar Navnet *A. Claparèdi*, stemmer overens med vor Art [i.e. *A. marina*] i, at Gjællerne begynde paa syvende børstebærende Ring og strække sig over 13 Ringe, men afviger fra den ved følgende Karakterer: Gjæller, som kun i et meget kort Stykke ere forbundne ved Grunden, langstrakte, med 10 Par Grene; Rygbørster med meget svagt udviklede Haar, Bugbørster med stærkere tilspidset, lidt afsat, Endedeel."

[2] Which, however, he believed were represented by a pair of crypts near the origins of the metastomial grooves.

nuchal organ. There are six pairs of nephridia, opening on the fourth to ninth segments, twelve oesophageal glands, six on each side, and no septal pouches. Careful search failed to reveal the presence of stato-

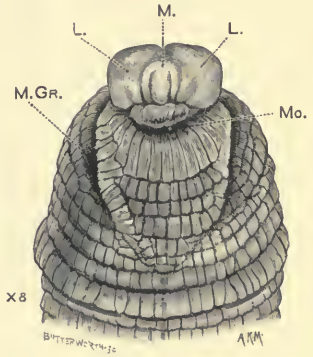

Fig. 51.

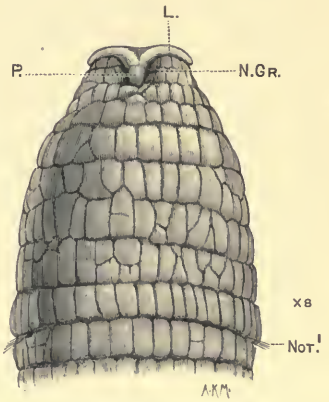

Fig. 52.

Figs. 51, 52.—*A. pusilla.* Type specimen, antero-ventral (Fig. 51) and dorsal (Fig. 52) views of the anterior end. In Fig. 51 all the parts, except the prostomium, are seen somewhat fore-shortened. L, Lateral lobe of prostomium; M, Median lobe; M.GR, Metastomial groove; MO, Mouth; N.GR, Nuchal groove; NOT[1], First notopodium; P, Median posterior portion of prostomium.

cysts, and the writer believes them to be absent.[1] The type was compared directly, point by point, with a long series of examples of

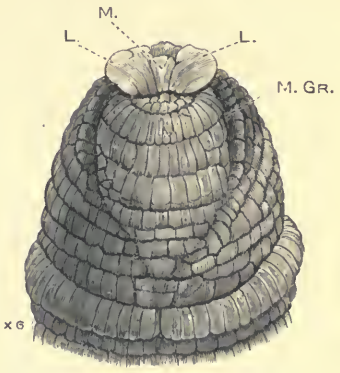

Fig. 53.

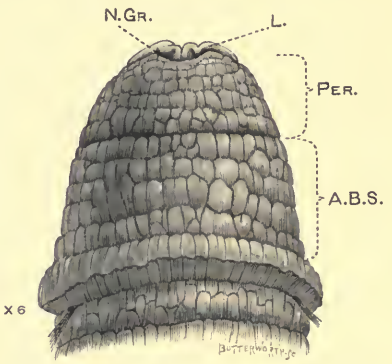

Fig. 54.

Figs. 53, 54.—*A. pusilla.* Specimen from California, antero-ventral (Fig. 53) and dorsal (Fig. 54) views of the anterior end, for comparison with Figs. 51, 52. PER, Peristomium; A.B.S, Achaetous body-segment (note the strongly developed groove between these segments, see p. 37).

A. cluparedii. The anterior end of one of these, from Crescent City, California, is represented in Figs. 53, 54, which show that, making due

[1] To establish, beyond doubt, the absence of statocysts, it would be necessary to make serial sections of the anterior end, a course which is obviously precluded in this case.

allowance for some contraction of the oral region and compression of the median prostomial lobe, this specimen and *A. pusilla* have prostomia of an identical type. They agree also in their internal organs, except that in *A. claparedii* there are typically only five pairs of nephridia; but this difference is not sufficient to justify the separation of two otherwise identical forms, as it may be an individual or a local variation.[1] The writer two years ago reached the conclusion, which subsequent examination of further material has amply confirmed, that *A. pusilla* and *claparedii* are identical, and the two species are therefore merged under the older name.

Observations on the Records.—Prof. Child's specimens of "*A. marina*" were those afterwards examined and recorded by Dr. H. P. Johnson as *A. claparedei*. The Neapolitan specimens examined by Claparède and Jaquet, and those recorded by Lo Bianco, were examples of *A. pusilla*; Jaquet's figures show that several oesophageal glands and five pairs of nephridia were present, and that statocysts were absent—characters which apply only to *A. pusilla*. *A. marina* does not occur at Naples.

The two specimens on which Prof. Ehlers' record from Puerto Montt was based, which are in a bad state of preservation, have been carefully examined by the writer. In the number of their segments, the number and position of their gills, in the presence of short neuropodia—the only external characters[2] preserved—and in the number of oesophageal glands and absence of septal pouches, these specimens agree with *A. pusilla* and *assimilis* var. *affinis*. Statocysts could not be found, although the anterior end of one of the worms was cut into serial sections; the preservation was, however, so defective that it is possible the statocysts had disappeared owing to maceration. The writer has recorded these specimens as *A. claparedii* (= *pusilla*), and it seems advisable to retain this record with a query, and with the proviso that there is some possibility that the specimens may be *A. assimilis* var. *affinis*.

Prof. von Marenzeller's material of "*A. marina*" from several localities included specimens from Naples and Vancouver Island. The writer has recently examined one of the Vancouver examples,

[1] Such a variation is seen in the number of nephridia in *A. assimilis* var. *affinis*; examples from South Africa have only five pairs, while those from South America, New Zealand and Tasmania possess six pairs.

[2] The crotchets were worn, and did not serve to decide the identity of the species; in their characters they were not typical of *A. pusilla*, but tended towards those of *A. assimilis*.

which proved to be *A. pusilla.* Among the localities given by Ives for "*A. marina*" are Coquimbo and Vancouver, but the records from both these places relate to *A. pusilla.*

The specimen from Ossero, referred by Grube to "*A. piscatorum,*" which is preserved in the Kgl. Zoologisches Museum, Berlin (Ashworth, 1910), is an example of *A. pusilla.*

Grube's record from Callao is a mere mention of the specific name *A. piscatorum.* The writer has endeavoured, without success, to trace the material on which the record was founded; it is not in the museums of either Copenhagen or Berlin. The record is cited under *A. pusilla* on the ground that Callao lies within the known range of this and of no other species.

In the "Collection Grube" in the Berlin Museum are specimens—probably those collected by Grube and mentioned in his two memoirs (1838, 1840)—labelled "Mittelmeer," which belong to the species *A. pusilla.* Among the localities cited by Grube are Naples, Italy, Sicily, and on the ground of the inclusion of the first named, as well as on the result of the examination of his specimens, his record is included *pro parte* under this species.

Schmarda recorded examples from the Mediterranean, the English Channel and the Pacific Coast (the Bay of Paita, or Payta, Peru), and remarked that they all belonged to the same species, *A. piscatorum.* The subsequent statement that the specimens from Paita possessed twenty oesophageal glands shows that they were either *A. pusilla* or *assimilis.* Although the author has endeavoured to trace Schmarda's specimens he has failed to find them, so their identity cannot be established with certainty. Prof. Ehlers has included Schmarda's record under *A. assimilis,* but the respective distributions of *A. pusilla* and *assimilis* suggest that Schmarda's specimens more probably belonged to the former species, and his record is therefore cited here with a query.

Prof. Ehlers' record of *A. assimilis* from California is based on a specimen—a duplicate from Agassiz's collection—in the Göttingen Museum. Agassiz's collection is at present in the writer's hands, and from it was selected the example shown in Figs. 53, 54, p. 118. The Göttingen specimen has been compared directly with this and found to agree in every respect; it is undoubtedly *A. pusilla.*

The information given by Delle Chiaje regarding his specimens of *Lumbricus marinus* is very imperfect and unsatisfactory. The specimens were collected near Naples, and among them was apparently one or more with the first gill on the seventh segment, and therefore

belonging probably to the species *A. pusilla*. The description and figures are, however, in agreement with *A. branchialis* in several striking points, namely, the absence of tail and of dilatation of the anterior region of the body, the repeated *dichotomous* branching of the gills, the single pair of oesophageal glands and the size and shape of the septal pouches. It is clear from Delle Chiaje's later memoir (1841) that he did not, even then, recognise the difference between a caudate and an ecaudate *Arenicola*, for he referred specimens, some of which were undoubtedly *A. branchialis*, to the species *A. piscatorum*. It is probable that the earlier record also referred in part to *A. branchialis*. The carelessly drawn figure in Delle Chiaje's memoir formed the basis for the genus *Chorizobranchus* (see p. 32).

Bionomics.—*A. pusilla* is moderately common in shallow water, down to about six mètres, in parts of the Bay of Naples, where the bottom is muddy; it is abundant where organic matter is plentiful, *e.g.* near the outfall of drains. Lo Bianco states that in summer the worm either disappears or is found only rarely.

The general habits of this species, which the writer had an opportunity of observing in Naples for some weeks, are similar to those of *A. marina*.

Examples taken by Prof. A. D. Howard in Puget Sound were found generally in ordinary sandy beaches, but two larger specimens were burrowing in a coarse gravelly and rocky beach.

Size.—Neapolitan specimens are usually small—not more than 60 to 70 mm. in length. Lo Bianco states that they may attain a length of 150 mm., but that is an exceptional size; the writer has not seen, among the numerous Neapolitan specimens he has examined, any exceeding 100 mm. in length.

Examples from the Pacific attain a greater size—130–175 mm. in length.[1] Those from Dutch Harbour, Unalaska, are the largest known examples of the species; their length, 160 mm., is not remarkable, but they are of very massive build, being 50 to 60 mm. in girth at the widest point.

Colour.—Small Neapolitan specimens are pink and semi-transparent, so that the blood-vessels and internal organs can be well seen. In most cases there is a darkening, a "smoky" appearance,

[1] One reaches the length of 207 mm., but its tail is of extraordinary length (117 mm.), probably due to extreme relaxation *post-mortem*.

at the anterior end; the tail is generally yellow—chrome to gamboge—and the gills light red.

Large specimens are reddish brown in the middle region, their anterior end is often yellowish or darkened, the tail is yellow or greenish yellow, and the gills reddish brown.

The American specimens had apparently been, in life, darker in colour; some are brown (in alcohol or formalin), but others, especially those from California, are very dark—almost black, and similar in colour to preserved specimens of the dark variety of *A. marina* (*cf.* Pl. I. Fig. 3).

Variations in the Organs.—The varied forms assumed by the prostomium may be seen on reference to Figs. 51–54, 48, 49).

In examples from the coast of California there is a strong tendency to the reduction and loss of the first gill. Out of seven specimens from that coast only two have the full number of gills, and in one of these the right and left first gills are very small; specimens from other localities possess practically constantly the full number of gills.

There is a clear, and sometimes a striking, difference in the number of oesophageal glands exhibited by Mediterranean and Pacific specimens. The former seldom have more than four pairs, or at the most five pairs of caeca (Pl. VIII, Fig. 18), whereas the writer has seen only one American example with as few as five pairs, others had six to ten pairs (Pl. XIII, Fig. 44), and Dr. Johnson records specimens with fifteen and sixteen pairs.

Period of Maturity, Development.—Lo Bianco (1909) stated that *A. pusilla* is sexually mature, in the Bay of Naples, from November to May. The writer found that artificial fertilisation was successful from April 19th to May 16th, 1900, and that worms collected after the latter date had shed their genital products.

Nothing is known of the form in which the ova are deposited. The egg-cleavage and young larvae (p. 74) have been described by the writer, but later larval stages and post-larvae are unknown. It is remarkable that, in spite of the daily tow-nettings taken in the Bay of Naples, and the careful examination to which the plankton is subjected in the Zoological Station, the post-larval stages of *A. pusilla* have not been met with. Possibly the habitat of these stages is different from that of the corresponding phases of *A. marina* and *A. assimilis*, and they do not come into the surface waters.

The writer found, in mud dredged near Naples (May 15, 1900), a very small example, 7 to 8 mm. long, which already possessed the full number of branched gills and four pairs of oesophageal caeca. The nephridia had also assumed practically the adult form, but the prostomium was in a transitional condition.

Distribution.—*A. pusilla* is known to occur in Europe only at Naples and at Ossero (on the Island of Cherso) in the Adriatic.[1] It is possible that some of the records credited to *A. marina* from the Mediterranean (see p. 93) relate to the present species.

A. pusilla has been obtained at several stations on the western seaboard of America, namely, the Aleutian Islands (Amchitka, Atka, Unalaska), Vancouver Island, Puget Sound, Crescent City and Humboldt Bay, Cal., and Coquimbo (Chile). Examples recorded (under the name *A. piscatorum*) from the Bay of Paita, Peru, were probably *A. pusilla*, and two specimens from Puerto Montt, Chile, are placed provisionally in this species. The writer has seen two examples of *A. pusilla* from North Japan.

The records suggest that this species is present generally on the shores of the North Pacific, and that it extends well down the west coast of South America. How far the species extends into the Behring Sea and along the Coast of Siberia [2] is unknown.

Type specimen in the Muséum d'Histoire Naturelle, Paris.

Naples	Ashworth Coll.	1912. 4. 9. 27.
Dutch Harbour, Unalaska . .	,, ,,	1912. 4. 9. 28.
San Juan Island, Puget Sound .	,, ,,	1912. 4. 9. 29.

Arenicola assimilis Ehlers, and var. *affinis* Ashworth.

Plate VII, Fig. 16; Plate X, Fig. 29; Pl. XIII, Fig. 45; Pl. XIV, Fig. 50.[3]

Arenicola assimilis Ehlers.

Arenicola assimilis, *partim*—
Ehlers, Polych., in Hamb. Mag. Sammelr., ii, 1 (1897), p. 103; Fests. K. Ges. Wiss. Göttingen (1901), pp. 176, 177.

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[1] Careful search for this species has been made at Palermo and near Messina, but without success. Prof. C. Viguier, Director of the Zoological Station, Algiers, has informed the writer that he has not seen *Arenicola* in that neighbourhood.

[2] See remarks on a specimen from Siberia on p. 93.

[3] For other figures of this species, see Figs. 14, 22, pp. 46, 51, chaetae of adult; Fig. 21, p. 50, crotchets of post-larva; Fig. 38, p. 68, statocysts.

Arenicola assimilis—
Ashworth, Q. J. Micr. Sci., xlvi (1903), p. 740; Mitt. Zool. Mus. Berlin, iv (1910), p. 351; Proc. U.S. Nat. Mus., xxxix (1910), p. 17.

Arenicola marina oder ein sehr naher Verwandter—
Michaelsen, Reiseber., in Hamb. Mag. Sammelr., i (1896), p. 9 (Punta Arenas).

Caudate *Arenicola* with twenty chaetiferous segments; thirteen pairs of gills,[1] the first, which is on the eighth segment, may be small or absent; median lobe of prostomium moderately large, the lateral lobes in the form of a V, the limbs of which are of uniform thickness, that is, not dilated anteriorly though they may be bent; neuropodia clearly visible in each segment, those of the branchial region are short and do not approach the mid-ventral line; post-rostral region of the crotchets not dilated (contrast *A. pusilla*); six pairs of nephridia, which open on the fourth[2] to the ninth segments; several (six to sixteen) pairs of oesophageal glands, the anterior pair long and slender, the others smaller and more or less pear-shaped; septal pouches absent; a pair of large statocysts, each with tube to the exterior; statoliths numerous.

Arenicola assimilis var. *affinis* Ashworth.

Arenicola assimilis var. **affinis**—
Ashworth, Q. J. Micr. Sci., xlvi (1903), p. 764 (Otago Harb.; Macquarie I.; Falkland Is.); Mitt. Zool. Mus. Berlin, iv (1910), p. 351 (Susanna Cove; Kerguelen); Proc. U.S. Nat. Mus., xxxix (1910), p. 18 (Stewart I., N.Z.); Ann. S. Afr. Mus., xi (1911), p. 18 (Table Bay; Lüderitzbucht; Plimmerton, N.Z.; Tasmania).
Benham, Subant. Is., New Zeal., Art. xi (1909), p. 246 (Campbell I.).
Ehlers, Discovery Rep., vi (1912), Polych., p. 25 (Auckland I.).

Arenicola assimilis—
Ehlers, Zool. Jahrb., Suppl. v (1901), p. 265 (Susanna Cove).

Arenicola assimilis, *partim*—
Ehlers, *op. cit.* (1897), p. 104; Fests. K. Ges. Wiss. Göttingen (1901), p. 178.

Arenicola claparedii—
Pratt, Mem. Proc. Manchester Lit. Phil. Soc., xlv (1901), 13, p. 12 (post-larva).

Arenicola claparedi Lev. ?—
Ehlers, Abh. K. Ges. Wiss. Göttingen, Math. Phys. Kl., N. F., v, 4 (1907), p. 21 (Warrington,[3] N.Z.).

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[1] All the specimens of *A. assimilis* (typical form), and those of the variety *affinis* from Auckland Island, have bushy gills; all other examples of the variety have been found to have pinnate gills.
[2] In South African specimens of the var. *affinis*, *fifth* to ninth.
[3] ? Wellington.

Fig. 55. — *A. assimilis*, co-type, from Uschuaia. Anterior end, dorsal aspect; the prostomium is in a state of normal extension.

Fig. 56.—*A. assimilis* var. *affinis*, from Otago Harbour, N.Z. Anterior end, dorsal aspect; the buccal mass and pharynx are fully protruded, and the prostomium is well extended ST.O. External aperture of statocyst.

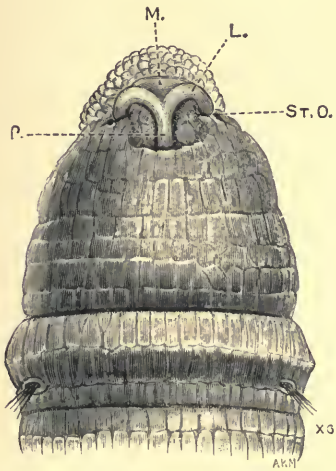

Fig. 57.—*A. assimilis* var. *affinis*, from the Falkland Islands. Anterior end, dorsal aspect; showing prostomium very fully extended, exposing to view the median posterior part (P.), which is usually hidden in the nuchal organ; M. Median; L. Lateral lobe of prostomium; ST.O. External aperture of statocyst.

Fig. 58.—*A. assimilis* var. *affinis*, from Susanna Cove. Anterior end, dorsal aspect; the lateral lobes of the prostomium are larger than usual, but are still considerably smaller than those of *A. pusilla* (*cf.* Fig. 48).

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Arenicola marina, *partim*—
Marenzeller, Zool. Jahrb. Abt. Syst., iii (1888), p. 12
Ives, Proc. Acad. Nat. Sci. Philad. 1890 (1891), p. 74.

Arenicola piscatorum Cuv. [*sic*] var.—
Grube, Monatsb. K. Preuss. Akad. Wiss. Berlin 1877 (1878), p, 511 (Kerguelen).

The variety *affinis* has nineteen segments; thirteen pairs of gills, the first, which is on the seventh segment, may be small or absent. Other characters as given above (p. 124).

Historical Account.—The species *A. assimilis* was founded by Prof. Ehlers on examples collected by Dr. Michaelsen in the Strait of Magellan. Prof. Ehlers stated that these worms appeared to be so closely similar to *A. marina* that, at first sight, he took them for examples of this species, but the presence of the first gill on the eighth segment, together with the provenance of the specimens, seemed to him to justify their separation from *A. marina*, as a closely allied species. He also remarked that the middle prostomial lobe seemed to be proportionately smaller in these specimens than in *A. marina*, and the dorsal chaetae more feebly "feathered." In 1901 Prof. Ehlers stated that the gut, vascular system and nephridia of *A. assimilis* agreed, as far as he had been able to ascertain, with those of *A. marina*, but there were differences in regard to the statocysts, and the position of the external apertures of these organs, which were apparently nearer the brain in *A. assimilis*.

The writer (1903) gave a full account, with figures, of the anatomy of *A. assimilis*, based on the study of co-types from Uschuaia and Punta Arenas, and showed that this species has twenty[1] chaetiferous segments, that the prostomium differs in form from that of *A. marina*, that the oesophageal glands are multiple, septal pouches are absent, the ventral lips of the nephridia are peculiarly frilled, and that the statocysts are remarkable for their large size. He also described examples from Otago Harbour, New Zealand, and Macquarie Island, belonging to the species *assimilis*, but differing from the type in having nineteen chaetiferous segments, and statoliths of purely external origin[2]—quartz grains, etc. The

[1] This unusual number of segments was not the subject of comment by Prof. Ehlers; he seems to have been more impressed with the unwonted position of the first gill.

[2] Those of the Fuegian specimens were spherical, and composed almost entirely of secreted substance.

latter difference, which was discussed in its taxonomic bearings, was regarded as unimportant (see p. 69). The difference in number of segments between the Fuegian and New Zealand examples, though striking, was not thought to be sufficient to justify the erection of a new species, in view of the fact that in all other points the two series of examples presented complete agreement. The presence in *A. assimilis* of two forms, one with twenty, the other with nineteen chaetiferous segments, seemed, however, to call for some recognition, seeing that in other caudate species the number of chaetiferous segments is constant. The New Zealand specimens were therefore referred to a new variety, to which the name *affinis* was given, indicating its close connection with, and resemblance to, the type. In the same memoir were described, from the Falkland Islands, post-larval and adult specimens, the latter agreeing with those from New Zealand except in the form of the statoliths. From the series of examples studied a full diagnosis of the species was given.

Observations on the Records.—Prof. Ehlers, in his original account, recorded examples of *A. assimilis* from Punta Arenas, Uschuaia, Lapataia Nueva, South Georgia and California. The adult specimens from Punta Arenas,[1] Uschuaia [1] and South Georgia[1] have twenty chaetiferous segments, and are typical examples of the species. Those from Lapataia Nueva[1] and a young abranchiate specimen, 6·5 mm. long, found among the "roots" of seaweeds at Uschuaia,[2] have nineteen segments, and are thus referable to the variety *affinis*. The inclusion of California in the range of distribution of this species is erroneous, for it rests on a specimen in the Göttingen Museum which Prof. Ehlers referred to *A. assimilis* solely because he found it to agree with this species in the arrangement of its gills (of which there were only twelve pairs). The writer has shown (p. 120) that this specimen belongs to the species *A. pusilla*.

Prof. Ehlers' second memoir gives an additional station for the species, namely, Susanna Cove. The writer has examined the original

[1] The writer has examined the original specimens from these stations, preserved in the Naturhistorisches Museum, Hamburg.

[2] This is the only station from which both the typical form and the variety (represented by a single post-larval specimen) have been recorded. Adults of the typical and varietal form occur, however, not far from one another in the Beagle Channel—at Uschuaia and Lapataia Nueva respectively, and in the Strait of Magellan, at Punta Arenas and Susanna Cove respectively.

specimens, which have nineteen segments, and thus belong to the variety *affinis*. In this memoir Prof. Ehlers makes the following statement: "*Arenicola assimilis* Ehl. kommt im antarctischen Kreise und im magellanischen Gebiete vor; ebenso an der chilenischen Küste, denn die von Schmarda erwähnte *Arenicola piscatorum* von 'den Küsten der Südsee' ist nach Ausweis eines der Schmarda'schen Stücke der Sammlung des Zoologischen Instituts in Wien *Arenicola assimilis;* und die Fundortsangabe des Thieres heisst hier Chile. Die Art tritt an der kalifornischen Küste wieder auf; ob eine litorale Verbindung zwischen dem nördlichen und südlichen Verbreitungsgebiete besteht, bleibt noch zu erweisen; sollte *Arenicola pusilla* Qtrfgs. von Coquimbo mit *Arenicola assimilis* Ehl. zusammenfallen, so wäre damit, wie mit dem Schmarda'schen Funde, eine Anbahnung gegeben." The specimen from the Californian coast, erroneously referred to the species *A. assimilis*, has been discussed above. The writer addressed to Prof. Grobben enquiries for the specimen of Schmarda mentioned by Prof. Ehlers, and he replied that in the catalogue of the collection in the Zoological Institute of Vienna there is no mention of an *Arenicola* collected in the Bay of Paita.[1] There is in the Vienna collection a specimen of "*A. piscatorum* aus Chile," but this was not obtained by Schmarda. His record states definitely that his specimens were taken in the Bay of Paita, which is on the most northerly portion of the coast of Peru, about a thousand miles north of the nearest point of the Chilian coast. It seems clear, therefore, that the Vienna specimen "aus Chile" has nothing to do with Schmarda's record. This specimen is recorded under *A. marina* (p. 94), to which species it undoubtedly belongs. It is more probable, judging from the distribution, that the specimen or specimens found by Schmarda in the Bay of Paita belonged to the species *A. pusilla*, for this bay is within the known range of *A. pusilla*, but is more than three thousand miles north of the nearest station from which *A. assimilis* has been recorded with certainty.

The example recorded by the writer from Kerguelen is that formerly recorded by Grube (*loc. cit.*) as "*Arenicola piscatorum* Cuv. var." Grube described this specimen as a variety of the common species because in most of the branchial segments he could distinguish only four, instead of the usual five, rings. The specimen is in very bad condition, but as it is the only one recorded hitherto

[1] Prof. Grobben was unable to state whether Schmarda's material was preserved or where it might be sought.

from that remote island[1] it is worthy of careful re-examination. The specimen is in three pieces, which, when joined together, are 208 mm. in length, of which the tail forms 74 mm. Assuming that all the parts are present, which is apparently the case, there are nineteen chaetiferous segments, the last thirteen of which bear gills. The writer is unable to confirm Grube's statement regarding the composition of the branchial segments, for, in each of the segments of this region in which the annuli are distinguishable, there are five, although one of them may be rather smaller than the others. The neuropodia are of the short type found in *A. assimilis* and *pusilla*. The outline of the prostomial lobes is sufficiently retained to show that the prostomium agrees with that of *A. assimilis*. Oesophageal glands are wanting, owing to damage, probably at the time of capture. Septal pouches were found to be absent. The number of nephridia cannot be ascertained on account of the damaged condition of the anterior nephridial region, and the search for statocysts was precluded by the leathery condition of the anterior end. The diagnosis rests, therefore, almost entirely on the form of the prostomium and the crotchets (Fig. 22 B, p. 51), but the writer has no hesitation in referring the specimen to the species *A. assimilis* var. *affinis*.

Prof. von Marenzeller recorded *Arenicola marina* from Angra Pequeña (Lüderitzbucht), but examination (Ashworth, 1911) of extensive well-preserved material from that bay, and of one of Prof. von Marenzeller's original specimens,[2] showed that the species which occurs there is *A. assimilis* var. *affinis*. Ives' statement that *A. marina* occurs in South Africa is based upon Prof. von Marenzeller's work.

[1] Since this account was finished M. Ch. Gravier has published notes on an example of *Arenicola* from Kerguelen (Bull. Mus. Hist. Nat. Paris, xvi (1910), p. 198; Ann. Inst. Océanogr., iii, fasc. 3 (1911), p. 35). The specimen was incomplete and in a very bad state of preservation. M. Gravier has referred it, but under great reserve, to *A. assimilis*. Prof. Ehlers has kindly informed me that among the collection made at Kerguelen by the German South Polar Expedition there is a specimen of *A. assimilis* var. *affinis*. Had M. Gravier's specimen been complete it would probably also have been found to belong to the variety *affinis*.

[2] This specimen was not in good condition at the anterior end, the outlines of the prostomial lobes were defectively preserved, statocysts could not be demonstrated, and only five pairs of nephridia were present, so it was recorded (Mitt. Zool. Mus. Berlin, iv (1910), p. 351) as *A. claparedii*. Subsequent microscopic examination of the stained and cleared anterior end showed that there were remains of a statocyst on one side (the rest of this organ and that of the other side had disappeared owing to maceration), and therefore the former determination was incorrect. The specimen is *A. assimilis* var. *affinis*, and agrees with all other South African examples of this species in having only five pairs of nephridia.

The examples from the Falkland Islands recorded by Miss Pratt were abranchiate post-larval stages, and were referred to *A. claparedii* because they possessed several oesophageal glands, a character which was at that time known only in, and believed to be diagnostic of, that species. The writer (1903) examined these specimens subsequently and showed that they were *A. assimilis* var. *affinis*.

The specimen from New Zealand, recorded by Prof. Ehlers as *A. claparedi* Lev.,? is in the British Museum. Though it is not in good condition its statocysts are demonstrable, and in its prostomium, nephridia and crotchets it agrees with other examples of *A. assimilis* var. *affinis* from New Zealand.

Habits, Size, Colour.—The habits of this species seem to be similar to those of *A. marina*. Dr. Michaelsen describes the occurrence in the sand flats near Punta Arenas of the "Sand- oder Fischer-wurm (*Arenicola marina* oder ein sehr naher Verwandter dieses Nordsee-Thieres)," with its worm-like castings, of almost pure sand, forming innumerable hillocks over wide stretches of the flats uncovered at low tide. These observations relate to the typical form of *A. assimilis*.

The seven specimens of *A. assimilis* (typical form) examined by the writer range in length from 110 to 160 mm. (the tail being 45 to 48 mm.). The examples of the variety *affinis* from the Falkland Islands and the southern extremity of New Zealand are about the same size as the foregoing. The largest examples are those from Macquarie Island and Kerguelen, which are 217 and 208 mm. long respectively (tail 85 and 38 mm. respectively), and the smallest are those from Tasmania, which are 46 to 58 mm. long.

Specimens, in alcohol or formalin, are brown, generally light brown, and have a similar appearance to preserved light-coloured examples of *A. marina*. A few have a rather darker tone, and some are yellower, especially those obtained in Table Bay, which Prof. Gilchrist states were of a striking yellow colour when alive.

Variations in the Organs.—Examples of *A. assimilis* from Fuegia, and of the variety from the Falkland Islands and from Auckland Island, exhibit a tendency to the reduction or absence of the first gill. None of the examples of the variety from Tasmania has gills on the seventh segment, and only two (out of seven) have gills on the eighth segment. The full number of gills is usually present in specimens from other localities.

The South African examples of the variety *affinis* afford a striking instance of variation, for nephridia are, without exception, absent in the fourth segment. In examples from other localities, nephridia are invariably present in this segment, and seldom (two out of twenty-four cases) show any marked reduction.

The oesophageal glands (Pl. XIII, Fig. 45) vary in number from six to sixteen pairs, and the number does not appear to be correlated with the size of the worm, for a specimen from Macquarie Island has seven pairs, while another, about half its length, from Susanna Cove, has fifteen pairs.

Period of Maturity, Post-Larval Stages.—The writer found that in specimens of *A. assimilis* var. *affinis*, taken in Otago Harbour about the end of August, 1902, the nephridial vesicles had been subjected to great distension, doubtless by the accumulation therein of genital products, shortly before capture of the worms. The post-larval example, recorded from Uschuaia by Prof. Ehlers, was found in October, 1892, so that there is a breeding season in that region also about the month of August.

The mode of deposition of the eggs and the early development are unknown. Only four post-larval specimens (see p. 80), all referable to the variety, have been recorded. Three of these were taken by Mr. R. Vallentin on the surface of the sea near the Falkland Islands, the fourth was found among "roots" of seaweeds at Uschuaia. All were abranchiate.

Distribution.—*Arenicola assimilis* has been recorded from Punta Arenas (Strait of Magellan), Uschuaia (Beagle Channel) and South Georgia. Specimens referable to the variety *affinis* have been found at the following stations[1]: Uschuaia (an abranchiate post-larva), Lapataia Nueva (Beagle Channel), Susanna Cove (Strait of Magellan); the Falkland Islands; Kerguelen; Otago Harbour, New Zealand, and islands to the south, namely, Stewart, Campbell, Auckland and Macquarie Islands; Plimmerton (near Wellington, N.Z.); Burnie, on the north coast of Tasmania; Table Bay and Lüderitzbucht, South Africa.

These records, which show that *A. assimilis* is a characteristically

[1] It is possible that two examples from Puerto Montt, Chile, recorded on pp. 115, 119 as *A. pusilla*, may be *A. assimilis* var. *affinis*, but, as no evidence of the presence of statocysts could be obtained in these badly preserved specimens, they have been placed provisionally in the former species.

southern species, are noteworthy in connection with the discussion on the former greater extent of the Antarctic continent.

Type specimen in Naturhistorisches Museum, Hamburg.

A. assimilis. (co-types) .	Uschuaia . .	Naturh. Mus. Hamb.	1912. 5. 25. 1/2.
Var. *affinis*			
,,	New Zealand . .	Prof. Benham, F.R.S.	1907. 5. 1. 31.
,,	Auckland I. . .	"Discovery" Exped.	1907. 5. 9. 48–50.
,,	Stewart I. . .	Ashworth Coll.	1912. 4. 9. 30.
,,	Burnie, Tasmania .	,, ,,	1912. 4. 9. 31.
,,	Lüderitzbucht .	,, ,,	1912. 4. 9. 32, 33.
,,	Falkland Islands .	,, ,,	1912. 4. 9. 34.

Arenicola ecaudata Johnston.

Plate II, Figs. 7, 8; Plate IX, Fig. 19; Plate XI, Figs. 34, 35; Plate XV, Figs. 52, 53.[1]

Arenicola ecaudata—

Johnston, Loudon's Mag. Nat. Hist., viii (1835), p. 566 (Berwick Bay); Catal. Worms Brit. Mus. (1865), pp. 231, 345.

Ashworth, Trans. Liverpool Biol. Soc., xi (1897), p. 30 (Port Erin); Fisheries Irel. Sci. Invest. 1908, vii (1909), p. 2 (Galway); Ann. Sci. Nat. Zool., sér. 9, x (1910), p. 114 (Kérity).

Beaumont, Proc. R. Irish Acad., ser. 3, v (1900), p. 784 (Valencia).

Bidenkap, Vid. Selsk. Forh. Christiania (1894), no. 10, pp. 39, 112 (Bergen; Hvidingsö).

Chenu, Illustr. conchyliol., i (1842), pp. 1, 12, pl. i, fig. 5.

Elwes, J. Mar. Biol. Assoc., N.S., ix (1910), p. 64 (Torquay).

Fauvel, C. R. Acad. Sci. Paris, cxxxv (1898), p. 733; Bull. Sci. France Belg., xxxii (1899), p. 289, etc.; Bull. Soc. Linn. Norm., sér. 5, ii (1899), p. 64 (Cherbourg); Mém. Soc. Nation. Sci. Nat. Math. Cherbourg, xxxi (1899), p. 163: (1900), p. 315.

Ferronnière, Bull. Soc. Sci. Nat. Ouest France, sér. 2, i (1901), p. 19 (Loire-Infér.).

Gamble and Ashworth, Q. J. Micr. Sci., xliii (1900), p. 432, pl. xxii, fig. 4.

Gemmill, Marine Worms, in, Fauna Clyde Area (1901), p. 361 (Cumbrae).

Koehler, Ann. Sci. Nat. Zool., sér. 6, xx (1885), Art. 4 (Jersey, Guernsey, Herm).

Lafont, Acta Soc. Linn. Bordeaux, xxviii (1873), p. 264 (Arcachon).

Lankester, Ann. Mag. Nat. Hist., ser. 3, xvii (1866), p. 390 (Herm).

M'Intosh, Rep. 39 Meet. Brit. Assoc. (1870), p. 90 (Plymouth); Ann. Mag. Nat. Hist., ser. 8, i (1908), p. 382 (Loch Maddy; Co. Dublin).

Malm, K. Vet. Handl. Göteborg, xiv (1874), p. 88 (Gullmarn; Löken; The Skaw).

Malmgren, Öfvers. K. Vet. Akad. Förh. 1867 (1868), p. 189 (Bahusia).

Mesnil, Zool, Anz., xxi (1898), p. 631; Bull. Sci. France Belg., xxxii (1899), p. 318 (C. la Hague).

Quatrefages, Hist. Nat. Annel., ii (1865), p. 265 (St. Vaast).

Storm, K. Norske Vid. Selsk. Skr. 1880 (1881), p. 95 (Trondhjemsfjord).

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[1] For other figures of this species, see Figs. 5, 6, 10, 28, pp. 40, 42, 56, chaetae of post-larval stages; Figs. 16A, 29, pp. 47, 57, chaetae of adult; Fig. 36, p. 61, gill.

Arenicola ecaudata, *partim*—
Ives, Proc. Acad. Nat. Sci. Philad. 1890 (1891), p. 74.

Arenicola boeckii—
Rathke, Nova Acta Acad. K. Leop.-Car., xx (1840), p. 181, tab. viii, figs. 19–22 (Trondhjem).

Arenicola bucci—
Hanna, Proc. Belfast Natur. Field Club, ser. 2, iv (1898), p. 425 (Antrim).

Arenicola branchialis, *partim*—
Fauvel, Proc. 4th Intern. Congr. Zool. (1899), p. 229.
Johnston, Catal. Worms Brit. Mus., p. 231.
Marenzeller, Zool. Jahrb. Abt. Syst., iii (1888), p. 13.
Mesnil, Bull. Sci. France Belg., xxx (1897), p. 163.
Michaelsen, J.-B. Komm. Wiss. Unters. Kiel, N.F., ii (1896), p. 136.
Saint-Joseph, Ann. Sci. Nat. Zool., sér. 8, v (1898), p. 391.

Lumbricus marinus, *another species*—
Dalyell, Powers Creator, ii (1853), p. 137, pl. xix, figs. 4–7 (Shetland).

Clymenides ecaudatus—
Mesnil, Bull. Sci. France Belg., xxx. p. 152 (St. Martin).

Ecaudate *Arenicola*, with first gill on the sixteenth[1] chaetiferous segment; thirteen pairs of nephridia, which open on the fifth to the seventeenth segments; gonads large, each gonad is produced, in the mature male, into one or more thin reniform outgrowths, and, in the mature female, into numerous digitiform or flattened processes.

Historical Account.—Johnston defined his new species in the following terms:—"*A. ecaudata*. Branchial tufts more than twenty pairs; the first fourteen or fifteen pairs of feet abranchial, tail none." There was, in the minds of some authors, considerable doubt as to the validity of this species, which was confused with *A. grubii* (= *branchialis*). Until 1898 there was no published reference to the internal organs of *A. ecaudata;* then appeared, in close succession, the observations of Drs. Gamble and Ashworth, and Profs. Mesnil and Fauvel, which finally dispelled all doubts regarding the autonomy of this species.

To Prof. Mesnil (1897) we owe the first description of the post-larval stages, which, however, believing them to belong to the genus *Clymenides*, he designated *C. ecaudatus*. Prof. Fauvel reared an example of "*C. ecaudatus*" into a young *Arenicola ecaudata*, and thus demonstrated their identity.

[1] The first gill is often small, and in about twenty per cent. of the specimens examined was wanting.

Observations on the Records.—Most of the records under *A. ecaudata*, being subsequent to 1898, were made in the light of the newer work on this species, and are thoroughly trustworthy. The earlier records to which definite localities are appended seem also to be reliable. Lafont's is the most southerly record for this species, and it is desirable that it should be ascertained definitely that the species occurring at Arcachon is really *A. ecaudata* and not *A. branchialis*.

Ives regarded all specimens of *Arenicola* with eleven to fifteen pre-branchial segments as *A. ecaudata*, the distribution of which he gave as "Europe, Mediterranean, Black Sea." It is abundantly evident that this "species" included *A. branchialis*.

Rathke's *A. bocckii* and Dalyell's "*Lumbricus marinus*, another species," were undoubtedly examples of *A. ecaudata*, with which they agree in their form and ecaudate character, and in the position of the first gill. Rathke's two examples were small and slender, the larger one was only 42 mm. long, but Dalyell's specimen was well grown, being about 215 mm. in length.

An examination of Mr. Hanna's original specimens of "*A. bucci*," which are small, proves their identity with *A. ecaudata*.

The statements of the authors cited under *A. branchialis* show that they have included therein *A. ecaudata*. Prof. Fauvel spoke, at the Zoological Congress of 1898, of *A. boeckii* as a synonym, and of *Clymenides ecaudatus* and *Branchiomaldane vincenti* as post-larval stages of *Arenicola branchialis*, but in the same year (*op. cit.*, 1898) realised that he had confused the two species *ecaudata* and *grubii* (= *branchialis*) under the name *branchialis*, and that *Branchiomaldane* was not a stage of either.

Johnston's idea of the characters of *A. branchialis* was evidently very hazy; in fact, he did not know the differences between it and *A. ecaudata*. Of the specimens he ranged under *A. branchialis*, three are mentioned, by the names *A. nodosa*, *montagui* and *dorvilliana*, as if they were synonyms. But these names ought not to have been included in the synonymy, as they were used by Leach in labelling specimens in his own collection; no description of these three "species," nor any further reference to them was published. These designations are *nomina nuda* and are therefore not included in the synonymy in the present work. The specimens labelled *A. nodosa* and *montagui* are still preserved, but "*A. dorvilliana*" is no longer in existence. "*A. nodosa*" is a complete and typical dark example, with bluish-green sheen, of *A. branchialis*;

"*A. montagui*" is a specimen of *A. ecaudata*, it is in bad condition and incomplete, but there is no doubt as to its species.

In the memoirs cited of Profs. Marenzeller, Mesnil, Michaelsen and Saint Joseph, "*A. branchialis*" included all the ecaudate forms then described—e.g. *ecaudata*, *bocckii*, *grubii*, etc.

Bionomics.—*Arenicola ecaudata* is not found burrowing in the ordinary sand of the beach like *A. marina;* it occurs in the littoral zone but chiefly in sandy, gravelly or muddy material among stones, or in clefts at the base of rocks in the débris formed by the breaking down of the latter. A considerable amount of organic matter is generally present in the material in which the worm lives. The burrows of *A. ecaudata* and *branchialis* are oblique or sinuous cavities, lined with a fair amount of mucus, and situated a few inches below the surface in gravel or between rocks and stones. The castings of the worm, being composed of coarse material having little coherence, soon fall apart. The well-known signs—the sand-rope-like heap of castings and the funnel-like depression in the sand—which indicate the presence of *A. marina* on countless sandy beaches, have no good counterparts in the case of the ecaudate species, in which both the castings and the mouth of the burrow are inconspicuous among their surroundings. Whether these species are present in any given area is therefore not obvious from a superficial examination, as is often the case where *A. marina* is concerned; their presence can only be ascertained after careful, and sometimes prolonged, search in likely places, such as those above described.

Little is known of the habits of *A. ecaudata* when it is covered with water, but observations of Prof. Fauvel[1] are of interest in this connection. He saw examples of *A. ecaudata*, which were kept in an aquarium, leave the sand during the night to wander about at the surface of the water, or to swim freely.[2] Each was surrounded by a thick envelope of mucus. On a light being brought near the aquarium, the worms at once began to burrow into the sand, leaving behind their mucous envelopes.

Size.—Average specimens of *A. ecaudata*, when normally extended are about 130 to 180 mm. long. The longest seen by the writer was 255 mm. in length. When at first withdrawn from their burrows

[1] Mém. Soc. Nation. Sci. Nat. Math. Cherbourg, xxxi (1899), p. 141.
[2] *Cf.* the remarks on the swimming of *A. marina*, p. 97.

the worms contract, but soon extend in well aerated water to nearly twice their reduced length.

Colour.—The colour of this species varies from dark brown or black, with greenish metallic sheen, to light reddish brown. Most of the British examples seen by the writer are of a yellowish red or brownish red tone, and with a purple anterior region, as shown in Pl. II, Fig. 7, but about one-third of the specimens collected are much darker, being coloured almost exactly like the example of *A. branchialis* figured on the same plate (Fig. 5).

Variations in the Organs.—The most striking variation is in regard to the number of segments. Adult specimens of this species seldom exhibit as many segments as they possessed at the end of the post-larval stage, but occasionally an unabbreviated example is met with, in which case the number of segments is about sixty to sixty-four. There are about forty-five to fifty segments in average specimens.

The number of gills depends, of course, chiefly on the number of chaetiferous segments, but even in unabbreviated specimens there may be some reduction in the gill-series anteriorly, or posteriorly, or at both ends. In about twenty per cent. of the specimens examined the normal first gill (that is, that on the sixteenth segment) was found wanting on both sides, and in a further twenty per cent. on one side. The last segment is not uncommonly abranchiate, and the writer has seen specimens with two, three, four, six and nine posterior abranchiate segments respectively.

Prof. Fauvel states that in his examples of *A. ecaudata* the number of nephridia is "12 paires, parfois 13," the last nephridium usually opening on the sixteenth segment, but all the British specimens examined by the writer possess thirteen pairs, and there was no sign of reduction of the last pair.

Period of Maturity, Development.—*A. ecaudata* was found to be mature, in the neighbourhood of Port Erin, during April, 1897, for the nephridial vesicles of specimens then dissected were greatly dilated with ova ready to escape. Ripe examples were obtained from Plymouth at the end of August, 1910, and from these Figs. 52 and 53, Pl. XV, were drawn. Whether there is for this species in Britain one continuous period of maturity, extending from the beginning of April to September, or there are two periods, separated by a non-breeding interval, the writer has not had the opportunity of

determining with certainty. Prof. Fauvel states that, in the neighbourhood of Cherbourg, the period of maturity of *A. ecaudata* extends through a considerable part of the year, for from the end of March to the beginning of October he has found individuals dilated with reproductive products.

Nothing is known regarding the form in which the eggs of this species are deposited. The early development is also unknown, the earliest stages observed being post-larval examples, about 4·5 mm. long, with about fifty chaetiferous segments. These are abranchiate and remain in that condition until about sixty fully formed segments are present, then gills begin to appear, generally on the sixteenth to nineteenth segments inclusive, and are subsequently formed on the following segments.

Post-larval stages range in colour from reddish or pale greenish yellow to dark green; the first two or three segments and the pygidium are generally darker than the rest of the worm. These stages are found near low-tide mark, among algae, for instance, among the "roots" of *Laminaria*, or in the crevices of *Lithothamnion*. When their gills have become well developed, and for the most part ramified, the worms leave the crevices in and among algae and begin to burrow in sand or gravel.

Most of the post-larval specimens recorded have been collected in July, August or September, but Prof. Fauvel has found them also in April, and M. Ferronnière in March. Mr. Southern took them in numbers in October, 1910, and obtained a single specimen in March, 1911. For an account of post-larval specimens see p. 80.

Distribution.—*Arenicola ecaudata* has been obtained from several widely separated British localities; it has been recorded from Shetland, Berwick, Devon and Cornwall, the Isle of Man, Cumbrae, Loch Maddy, and the writer has seen examples[1] from Loch Sween; in Ireland the species is known to occur in the north (Antrim), east (Co. Dublin), west (Galway and Mayo[2]) and south-west (Valencia and Crookhaven[2]).

This species has been found in the Channel Islands, and at several stations on the north coast of France, namely, in the neighbourhood of Cherbourg and at Kérity; on the west coast, it has been recorded from Finistère, the Loire estuary and Arcachon, this last being the

[1] In the collection of Prof. J. Graham Kerr, F.R.S.

[2] The specimens from Blacksod Bay, Mayo, and from Crookhaven were collected by Mr. R. Southern.

most southerly known locality for the species. *A. ecaudata* occurs on the Swedish coast near and to the north of Göteborg, and on the Norwegian coast at Hvidingsö (near Stavanger), Bergen and Trondhjem, this last being the most northerly station from which the species has been obtained.

A. ecaudata is therefore known from the coasts of north-western and western Europe as far south as about 45° N. lat.

Polperro, Cornwall . . .		62. 7. 12. 61.
Cornwall		72. 8. 30. 28.
Falmouth	W. C. Cocks.	50. 8. 20. 17.
("*A. montagui*") South Devon .	Mus. Leach.	Old Coll.
Plymouth	Norman Coll.	1912. 4. 8. 3.
Plymouth	,, ,,	1902. 7. 8. 69–71.
Plymouth		96. 7. 15. 17 & 18.
Bordeaux Harb., Guernsey . .	Prof. Jeffrey Bell.	89. 9. 16. 17.
Herm	,, ,, ,,	89. 9. 16. 9.
Millport	Ashworth Coll.	1912. 4. 9. 20.
Cherbourg (post-larval stage)	,, ,,	1912. 4. 9. 19.

Arenicola branchialis Audouin and Edwards.

(*A. grubii* Claparède.)

Plate II, Figs. 5, 6; Plate IX, Fig. 20; Plate XV, Fig. 51.[1]

Arenicola branchialis—

Audouin et Edwards, Ann. Sci. Nat., xxx (1833), p. 422, pl. xxii, fig. 13; Hist. Nat. Litt. France ii (1834), p. 287, pl. viii, fig. 13 (St. Malo).
Bobretzky, Mém. Soc. Nat. Kiev, i (1870), pp. 6, 248 (Black Sea).
Caillaud, Ann. Soc. Acad. Nantes, xxxvi (1865), p. 28 (Loire-Infér.).
? *Chenu*, Illustr. conchyliol., i (1842), pp. 1, 12, pl. i, fig. 6.
Fauvel, Bull. Soc. Linn. Norm., sér. 4, ix (1896), p. 141 (St. Vaast).
Johnston, Catal. Worms Brit. Mus. (1865), p. 345 (Cornwall).
Mesnil, Zool. Anz., xxi (1898), p. 631; Bull. Sci. France Belg., xxxii (1899), p. 318 (La Hague).
Quatrefages, Hist. nat. Annel., ii (1865), p. 265.

Arenicola branchialis, near to—

Gosse, Rambles Devon. Coast (1853), p. 174 (Watermouth).

Arenicola branchialis, *partim*—

Johnston, *op. cit.*, p. 231.
Marenzeller, Zool. Jahrb. Abt. Syst., iii (1888), p. 13.
Mesnil, Bull. Sci. France Belg., xxx (1897), p. 163.
Michaelsen, J.-B. Komm. Wiss. Unters. Kiel, N.F., ii (1896), p. 136.
Saint-Joseph, Ann. Sci. Nat. Zool., sér. 8, v (1898), p. 391.

Arenicola grubii—

Claparède, Annél. Naples (1868), p. 296, pl. xix, fig. 2; Mém. Soc. Phys. Genève, xx (1870), p. 36.
Allen and Todd, J. Mar. Biol. Assoc., N.S., vi (1901), p. 195 (Salcombe Esty.).

[1] For other figures of this species, see Fig. 3, p. 34, anterior end; Figs. 16B, 30, pp. 47, 57, chaetae; Fig. 35, p. 61, gill; Fig. 41, p. 70, statocyst; Fig. 42C, p. 72, ovum.

Arenicola grubii—*continued.*

Ashworth, Fisheries Irel. Sci. Invest. 1908, vii (1909), p. 2 (Galway); Mitt. Zool. Mus. Berlin, iv (1910), p. 353 (St. Malo; Roscoff; Nice; Lesina (Adriatic)); Ann. Sci. Nat. Zool., sér. 9, x (1910), p. 113 (I. Chausey; Tangier, Morocco).

Beaumont, Proc. R. Irish Acad., ser. 3, v (1900), p. 784 (Valencia).

Ehlers, Zeits. Wiss. Zool., liii, Suppl. (1892), p. 249, taf. xiii, figs. 33–37.

Fauvel, Bull. Sci. France Belg., xxxii (1899), p. 292 (Cherbourg); Mém. Soc. Nation. Sci. Nat. Math. Cherbourg, xxxi (1899), p. 166; Bull. Inst. Océan. Monaco (1909), no. 142, p. 8 (Berlinga Is.).

Gamble and Ashworth, Q. J. Micr. Sci., xliii (1900), pp. 429, 541, pl. xxii, fig. 3 (I. of Man; Jersey; Port Appin).

Horst, Notes Leyden Mus., xi (1889), p. 43, pl. iii, figs. 12–15 (gills, chaetae).

Jourdan, C. R. Acad. Sci. Paris, xcviii (1884), p. 757 (Marseilles).

Lo Bianco, Atti R. Accad. Sci. Fis. Mat. Napoli, v, ser. 2, no. 11 (1893), p. 10, tav. ii, fig. 2; Mitt. Zool. Stat. Neapel, xiii (1899), p. 484: xix (1909), p. 577.

Arenicola grubei—

Ferronnière, Bull. Soc. Sci. Nat. Ouest France, sér. 2, i (1901), pp. 39, 53 (Loire-Infér.).

Arenicola bobretzkii—

Czerniavsky, Bull. Soc. Imp. Nat. Mosc., lvi (1881), p. 355 (Sevastopol).

Arenicola cyaneus—

Czerniavsky, Trudi Soc. Nat. St. Petersb. (1868), p. 27 (Black Sea).

Arenicola cyanea—

Czerniavsky, *op. cit.* (1881), p. 354 (Alupka, Black Sea).

Arenicola dioscurica—

Czerniavsky, *op. cit.* (1881), p. 355 (Suchum, Black Sea).

Arenicola ecaudata—

Grube, Schles. Ges. Vaterl. Cultur, Abt. Nat. (1872), pp. 91, 106, 142 (St. Malo; Roscoff).

Arenicola ecaudata, *partim*—

Ives, Proc. Acad. Nat. Sci. Philad. 1890 (1891), p. 74.

Arenicola, eine andere Art –

Grube, Anat. Physiol. Kiemenwürmer (1838), p. 3 (Catania).

Arenicola piscatorum, *partim*—

Delle Chiaje, Descr. Anim. invert., v (1841), p. 100.

? Lumbricus marinus, *partim*—

Delle Chiaje, Mem. Anim. s. Vert., ii (1825), p. 423.

Ecaudate *Arenicola*, with first gill on the twelfth[1] chaetiferous segment; five pairs of nephridia, which open on the fifth to the ninth segments; gonads small, as in the caudate species.

Historical Account.—In 1833 Audouin and Milne Edwards recorded observations on *Arenicola piscatorum* and then proceeded to

[1] The first gill is often small, and is not uncommonly missing on one or both sides.

describe a new species—*A. branchialis*—regarding which they gave the following particulars: "Cette espèce, que nous avons rencontré près de Saint-Malo, est beaucoup plus petite que la précédente, et s'en distingue principalement par le nombre des pieds et des branchies. Ces derniers organes, au lieu de commencer au-dessus des pieds de la septième paire, ne se montre que sur l'anneau qui porte les pieds de la treizième ou quatorzième paire, et au lieu d'être au nombre de treize paires, on en compte de dix-neuf à vingt paires. Du reste, cette espèce ne nous a présenté rien de particulier." In the general description of the genus *Arenicola* the authors pointed out that this worm is divisible into three regions—(*a*) an anterior, abranchiate, and generally dilated, (*b*) a middle branchiferous, and (*c*) a posterior apodous. The reference letters, *a*, *b*, *c*, are placed alongside the corresponding regions in the figures of *A. piscatorum* and *branchialis*. The latter figure represents a specimen about 117 mm. long, in which are indicated thirty-one pairs of notopodia, beyond the last of which is a region (lettered *c*), about 9 mm. in length, without chaetae and gills. This region, consisting of six rings, of which the terminal one is the largest, is almost as long as the three preceding chaetiferous segments. The first right gill is shown on the fourteenth segment, the first left one on the thirteenth; there are eighteen gills on the right side of the worm and nineteen on the left.

It is not surprising that most subsequent authors inferred, from Audouin and Edwards' account, that in *A. branchialis* the occurrence of a "tail" of some extent was to be expected. Some writers greatly exaggerated the length of this region, for instance, Chenu figured a specimen, labelled *A. branchialis*, in which are shown thirty-one chaetiferous segments, the last nineteen of which are branchiferous, followed by a tail as long as the branchial region. Quatrefages added to the diagnosis of *A. branchialis* the statement "Cauda quartam partem corporis circiter aequans," and wrote (p. 266) that "l'A. branchiale, dont la région caudale est presque aussi développée que dans l'A. des pêcheurs," was distinguished by this character from *A. ecaudata*. Johnston stated that *A. branchialis* and *piscatorum* "agree in having an abranchial tail," and remarked that there was no complete specimen of the former in the British Museum collection. Probably the fact that none of the specimens exhibited such a tail as he expected to find induced him to regard them as incomplete. His ideas of the characters of *A. branchialis* were not clear, for the specimens which he labelled with this name include examples of both the ecaudate species (see pp. 134, 135).

In 1868 Claparède defined *Arenicola grubii* in the following terms—"Corpus longitudine 6–7 cent., latitudine 3–4 mm., nigrum obscure viridescens, segmentis anticis branchiis destitutis decem, posterioribus branchiatis viginti, cauda fere nulla." There is an error in this diagnosis, there being eleven, not ten, anterior abranchiate chaetiferous segments; Claparède overlooked the first, a mistake easily made because the first notopodium is often absent or minute. Claparède remarked on the similarity of his species to *A. branchialis*, but noted that in the latter the first pair of gills was said to be on the thirteenth or fourteenth segment.[1] He described the segmental organs, of which he found five pairs, the nervous system and statocysts, and noted the unilateral branching of the gills. The position of the first gill, the absence of tail, and the presence of five pairs of nephridia and of closed statocysts, serve to fix definitely the species with which he was dealing.

The brief and imperfect description of *A. branchialis* given by its founders has led to much confusion. Some writers have held that this species was so insufficiently described that its identity could not be established definitely; others considered it to be identical with *A. grubii*, and a few, believing *ecaudata* and *grubii* to be synonymous, have united them under the earlier name *branchialis*. This last view, based on a consideration of the gross external features only, became untenable immediately the internal organs of *A. ecaudata* were inspected. The differences between the two ecaudate species in the number of their nephridia and the nature of their gonads were first commented upon by Drs. Gamble and Ashworth (1898), and Prof. Mesnil shortly afterwards drew attention to differences in the number of segments and gills, and in the position of the first pair of gills. Accounts of the internal and external anatomy and of the differential characters of this species were given by Prof. Fauvel and by Drs. Gamble and Ashworth.

Nomenclature of the Species.—The possibility that *A. branchialis* and *A. grubii* were identical has not been overlooked, but most writers since the publication of Claparède's memoir (1868) have preferred to use for this species the name *grubii*, because it was associated with a description enabling the species to be at once identified.

The identity of *A. branchialis* cannot be determined by an appeal

[1] And that "Johnston, qui paraît décrire la même espèce sous le nom de *A. ecauda* [*sic*], l'indique même au quinzième ou seizième." Claparède evidently considered *branchialis* and *ecaudata* to be synonymous.

to the type specimen, as it is no longer in existence. The only authoritative information regarding the species is that given in the original account and figure. The embellishments added to the diagnosis by some subsequent writers, without reference to the type, are not admissible as evidence.

The figure of *A. branchialis* given by Audouin and Edwards represents an *Arenicola* with a short "tail," but with the characteristic form of the ecaudate species, that is, the worm is only a little dilated anteriorly. The writer has a number of specimens of *A. grubii* in which, behind the last chaetiferous annulus, there is a region, composed of three or four rings, about 6 mm. in length. The corresponding region in Audouin and Edwards' specimen is drawn about 9 mm. long. Their figure is almost certainly wrong in representing this terminal portion as cylindrical. It should have been conical. Making due allowance for this mistake, the figure shows a specimen of such a character that, were it now in existence, the writer has no doubt that it would be described as ecaudate, that is, in contrast to species like *A. marina*, in which a well-developed tail is present.

Having reached the conclusion that the specimen of *A. branchialis* was ecaudate, it may be stated at once that there is no reason to associate *A. branchialis* with *A. ecaudata*, for there is no known specimen of the latter with gills so far forward as the thirteenth, or even the fourteenth, segment. The first pair of gills in *A. ecaudata* is on the sixteenth segment, and, after examination of more than two hundred specimens, the author is convinced that a forward extension of the gills in this species,[1] so that they would correspond in position to those of *A. branchialis*, never occurs. The first pair of gills in *A. grubii* is normally on the twelfth segment, but not infrequently the gills of this segment are wanting, and the thirteenth is thus the first branchiate segment. The writer has seen more than a dozen specimens of *A. grubii* exhibiting this condition, and has one specimen in which the thirteenth segment bears a gill on the left side only. The fourteenth and succeeding segments are provided with paired gills. This specimen agrees exactly, in the position of its anterior gills, with that of *A. branchialis* figured by Audouin and Edwards. It has been shown already that the "tail" of *A. branchialis* is of the same nature as, and only slightly longer than, that present

[1] Only one specimen of *A. ecaudata* is known in which a forward extension of the gills has occurred; in this a small gill is present on the left side only of the fifteenth segment.

not uncommonly in examples of *A. grubii*. There is therefore no character by which *A. branchialis*, as described by Audouin and Edwards, can be distinguished from the examples of *A. grubii* above mentioned.[1] These two species are therefore merged under the earlier name *branchialis*.

Prof. Mesnil considered *A. branchialis* and *A. grubii* to be identical, and advocated a return to the former name for this species. He suggested that Audouin and Edwards had counted and figured an anterior abranchiate segment too many, and thus assigned the gills to a position one segment too far back. The writer cannot see any evidence of this in the figure, which represents the segmentation of the anterior end approximately accurately, and considers it much more probable that in Audouin and Edwards' specimen the anterior gills were wanting, as in that described above.

Observations on the Records.—Chenu's modification of the original figure by the addition of a tail as long as the branchial region was unwarrantable, and shows that his figure, instead of being from nature, was a composition. Gosse placed his specimen near *A. branchialis*, probably because the number of branchiate segments was not the same as in Audouin and Edwards', but it was evidently of this species. The five following citations refer to descriptions which include both caudate species under the name *A. branchialis* (see also p. 135).

The three species described by Czerniavsky from the Black Sea all possessed the eleven anterior abranchiate segments characteristic of *A. branchialis*, and differed from one another only in colour and in the number of branchiate segments, of which they had twenty, thirteen and fifteen respectively. The type specimen of *A. bobretzkii* is no longer in existence, but the writer has had a dozen examples from the same locality—the Bay of Sevastopol—all of which are *A. branchialis*. By the courtesy of Prof. Nassonow the author has been enabled to examine the types of *A. cyanea*[2] (= *cyaneus*) and *dioscurica*, which are preserved in the Zoological Museum of the

[1] The writer has reached this conclusion only recently, and after examining a long series of specimens, in which he found the examples cited above with reduced gills and those with the terminal region more elongate than usual. When Pl. II was printed, early in 1909, he was of opinion that the identity of *A. branchialis* and *grubii* could not be established *with certainty*, and that therefore the correct name of the species was *A. grubii*.

[2] The much inflated anterior ring, mentioned in Czerniavsky's description of this species, is the protruded pharynx.

Imperial Academy of Sciences, St. Petersburg. They are both undoubted *A. branchialis.*

The three specimens recorded by Grube, from Saint-Malo and Roscoff, as *A. ecaudata*, are preserved in the K. Zoologisches Museum, Berlin, and have been shown by the writer to be examples of *A. branchialis.*

Ives' definition of the "species" *ecaudata*—with eleven to fifteen pre-branchial segments—and the localities cited—Europe, Mediterranean, Black Sea—show that *A. branchialis* was included.

The Catanian *Arenicola* described by Grube had thirty-eight segments, the first eleven of which were abranchiate, and it therefore belonged to this species.

In Delle Chiaje's account of his examples of "*A. piscatorum*," the chief characters mentioned are that the worms were reddish yellow, and had thirty-one chaetiferous segments, thirteen to twenty of which bore bi- or tri-partite gills. A specimen with thirty-one segments and twenty pairs of gills would have the first pair on the twelfth segment, as in *A. branchialis*, and no doubt some of the specimens belonged to this species. Those with thirteen pairs of gills may have been examples of *A. pusilla.*

The unsatisfactory nature of the information given by Delle Chiaje regarding "*Lumbricus marinus*" has already been noticed (pp. 120, 121), and the reasons stated for believing that his series of specimens included one or more *A. branchialis.*

Bionomics.—The habits of *Arenicola branchialis* are similar to those of *A. ecaudata* (see p. 135), and the two species have been frequently taken together. *A. branchialis* is usually found in oblique or sinuous cavities[1] in coarse, sandy or gravelly material, among stones about the mid-littoral zone. Like other species, *A. branchialis* is more plentiful in situations in which organic matter is abundant; for instance, in the Bay of Naples this species lives by preference near the mouths of drains, where it is very common (Lo Bianco). Prof. Fauvel found *A. branchialis*, near Cherbourg, in black muddy sand which gave off an offensive odour; the worms were so abundant there that they were collected for use as bait.[2] This species is, however, seldom found in such large numbers, or obtained so easily, as to make its collection for bait worth the labour required.

[1] Saint-Joseph (*loc. cit.*) found a specimen of *A. branchialis*, at St. Jean de Luz, in the sand, in a U-shaped burrow similar to that of *A. marina.*

[2] Bull. Soc. Linn. Normandie, sér. 5, ii (1899), p. 67.

Size.—Average British or French specimens of *A. branchialis* are about 150 mm. long, when extended normally; the longest seen by the writer reached a length of 250 mm. Specimens from Naples and the Black Sea have a thinner body wall and are less robust than the preceding, and seldom exceed 100 mm. in length.

Colour.—Examples of *Arenicola branchialis* from the Atlantic shores of Great Britain, France, Spain and Northern Africa, range in colour from bluish black to dark green, brown, and light reddish brown, but the majority are very dark. The specimen represented in Pl. II, Fig. 5, exhibits the typical colouration of British specimens, and indicates the greenish iridescence so frequently associated with the anterior region. A few examples from the localities above named exhibit lighter colours, similar to those shown in the figure of *A. ecaudata* on Pl. II, Fig. 7.

Neapolitan specimens are generally dark iridescent green in their anterior and posterior regions, and dark reddish brown in the middle region of the body, but occasionally a lighter specimen—yellowish red in colour—is met with.

Variations in the Organs.—The number of segments is subject to much variation; most specimens have lost some of their posterior segments and thus exhibit fewer than they possessed at the end of the post-larval stage, when forty to forty-three were present. The number of segments in this species is therefore about twenty fewer than in *A. ecaudata*, in which there may be sixty to sixty-four. Average specimens of *A. branchialis* have about thirty segments. The gills are liable to reduction anteriorly (see p. 142) and posteriorly, the last one to four segments being not uncommonly abranchiate.

The first notopodium is either minute or wanting in about 30 per cent. of the specimens examined, but the corresponding neuropodia are well developed (Pl. II, Fig. 6).

Period of Maturity, Development.—In the Irish Sea and the English Channel the breeding season is about September to October. Lo Bianco states that this species is mature at Naples in winter; specimens examined there by the writer at the end of March, 1900 and 1906, were found to have finished spawning.

The form in which the eggs are laid, and the larval development are unknown. The only known post-larval examples (described on pp. 81, 82) were collected by Mr. R. Southern, among the "roots" of *Laminaria*, in Blacksod Bay, Mayo, in September, 1910.

Distribution.—It is remarkable that *Arenicola branchialis* has not been recorded from any point on the shores of the North Sea.[1] The species is known from the following British localities—North and South Devon, Cornwall, the south-west of the Isle of Man, Millport, Port Appin (Loch Linnhe), Loch Maddy[2] (North Uist), Galway, Mayo,[3] Valencia, Port Stewart[3] (Londonderry), as well as from Jersey and Guernsey. It has been recorded from several points on the north coast of France, from Luc-sur-Mer to Roscoff, and also from the Loire estuary and St. Jean de Luz. This species also occurs at Santander,[4] and on the coast of Portugal at La Granja and the Berlinga Islands, and the writer has recently recorded examples from Tangier, Morocco. There is a specimen in the K. Zoologisches Museum, Berlin, said to be from the South Atlantic, but no nearer indication of the locality is given.

In the Mediterranean, *A. branchialis* occurs in the Gulf of Lyons, at Nice, Naples and Catania,[5] and at Triest and Lesina in the Adriatic. It has been recorded from three stations—Sevastopol, Alupka and the Bay of Suchum—on the northern shore of the Black Sea, but it apparently does not occur on the western shore of this sea in the vicinity of Varna.[6]

The distribution of *A. branchialis* may be summarised thus—this species is known from the Atlantic coasts of western and north-western Europe and Morocco, from several stations in the Mediterranean (south coast of France, Naples, Sicily), from the Austrian coast of the Adriatic and the northern shore of the Black Sea.

On a portion of the Atlantic seaboard of western and north-western Europe the two species *A. branchialis* and *ecaudata* are found together, but the former does not occur so far north[7] as the latter, and has not been found on the shores of the North Sea. But *A. branchialis* has been found about 10° further south than *A. ecaudata*, and extends into the Mediterranean, Adriatic and

[1] The station nearest to the North Sea from which this species has been recorded is Luc-sur-Mer (Calvados).

[2] Specimens in the collection of Prof. W. C. M'Intosh, F.R.S.

[3] Specimens collected by Mr. R. Southern.

[4] Specimens sent to the writer by Prof. Rioja y Martin.

[5] Careful search has been made for this species in the neighbourhood of Messina and Palermo, but without success. Prof. Viguier has informed me that he has not seen any specimen of *Arenicola* on the coast of Algiers.

[6] From information kindly given by Prof. B. Kurzius, of Sofia.

[7] The most northern station from which *A. branchialis* has been obtained is Loch Maddy, in North Uist, whereas *A. ecaudata* has been found as far north as Trondhjem.

Black Seas, from which *A. ecaudata* has not been recorded and in which it probably does not occur.

Polperro, Cornwall		62. 5. 5. 48–52.
Cornwall		68. 1. 17. 9.
("*A. nodosa*") [1] South Devon	Mus. Leach.	Old Coll.
Plymouth	Norman Coll.	1912. 4. 8. 4.
Port Erin, I. of Man	Ashworth Coll.	1912. 4. 9. 43–5.
Blacksod Bay, Mayo (end of post-larval phase)	,, ,,	1912. 4. 9. 40.
Naples	Norman Coll.	98. 5. 6. 17–19.
Mediterranean		85. 8. 10. 49.
Cette, Hérault	Ashworth Coll.	1912. 4. 9. 39.
Eudoume, Marseilles	,, ,,	1912. 4. 9. 41/2.
Sevastopol	,, ,,	1912. 4. 9. 38.
Santander	,, ,,	1912. 4. 9. 35–37.

BRANCHIOMALDANE Langerhans (1881).

BRANCHIOMALDANE VINCENTI Langerhans.

Plate XI, Figs. 31, 32, 33.

Branchiomaldane vincenti—
Langerhans, Nova Acta K. Leop.-Car. Akad., xlii (1881), p. 116, tab. v, fig. 21 (Teneriffe).

Branchiomaldane vincenti—
Ashworth, Proc. R. Soc. Edin., xxxii (1912), p. 62.
Gamble and Ashworth, Q. J. Micr. Sci., xliii (1900), pp. 536, 553.
Mesnil, Bull. Sci. France Belg., xxx (1897), p. 156 (St. Martin); xxxii (1899), p. 323; Zool. Anz., xxi (1898), p. 635.

Arenicola vincenti—
Fauvel, C. R. Acad. Sci. Paris, cxxvii (1898), p. 735; Bull. Sci. France Belg., xxxii (1899), p. 313; Mém. Soc. Nation. Sci. Nat. Math. Cherbourg, xxxi (1899), p. 165.

Clymenides incertus—
Mesnil, Bull. Sci. France Belg., xxx (1897), p. 154.

Adult.—Small, ecaudate, feebly-pigmented Arenicolidae, found living in mucous tubes among algae or on stones. Gills, consisting of one, two or three, rarely four, finger-shaped filaments, borne dorsally on the middle and posterior segments. The branchial segments are, for the most part, bi-annulate, being composed of a larger anterior chaetiferous and a smaller posterior branchiferous annulus. Prostomium large, nuchal groove shallow. Two pairs of nephridia, opening on the fifth and sixth segments, the second nephridium elongate and extending backwards into the seventh and eighth segments (or even further). Hermaphrodite, reproductive organs situated on the septa and oblique muscles. Statocysts absent.

[1] See pp. 134, 135, for remarks on this specimen.

Young Stages.—Similar in form to adults, but abranchiate. The annulation may not have made its appearance, and gonads are absent.

Historical Account.—This genus and species were based by Langerhans on some small worms which he found living in sand-covered tubes on the north shore of Teneriffe. He stated that, while these specimens exhibited unmistakable relationship with the Maldanidae, the presence of gills on a number of the posterior segments indicated that the worms should be placed in the family Thelethusae. Langerhans briefly described the anterior end, the chaetae and gills, and defined the genus thus: "Thelethusen mit einfachfadenförmigen Kiemen."

Prof. Mesnil gave some details regarding the segmentation of the body, the chaetae, gills and alimentary canal of a specimen of *B. vincenti*, which he had found at St. Martin, near Cape la Hague, and in 1898 published observations on other specimens, which he showed to be adult and hermaphrodite, and added a few notes on the early stages of development.

Prof. Fauvel at first[1] regarded *B. vincenti* as a post-larval stage of *Arenicola ecaudata*, but, on examining other specimens, he saw that they were adult. He considered *B. vincenti* to be anatomically an *Arenicola*—a dwarf *Arenicola* arrested at the "Branchiomaldane stage"—and therefore referred it to that genus as *A. vincenti*.

Drs. Gamble and Ashworth, after stating the results of their examination of two specimens of *B. vincenti*, concluded that the genus *Branchiomaldane* should be retained, and the writer, who has recently investigated the anatomy of the worm in detail, maintains this view.

Prof. Mesnil at first considered *Clymenides incertus* to be autonomous, but in 1898 expressed the belief that his specimens were young stages of *B. vincenti*. The writer has examined the original specimens, which are undoubtedly young *B. vincenti*.

External Features.—*B. vincenti* is an elongate, cylindrical worm, tapering slightly in its posterior half or third (Pl. XI, Fig. 31). It appears not to exceed a length of 20 mm., and most specimens are considerably shorter—about 7 to 11 mm. The prostomium is bluntly conical and overhangs the mouth. It bears dorsally and

[1] Proc. 4th Internat. Congr. Zool. (1899), p. 229; Bull. Soc. Linn. Normandie, sér. 5, ii (1899), p. liii.

laterally groups of eyes (Fig. 59), the number and disposition of which vary a little in different specimens. The peristomium, which is achaetous, is separated from the prostomium by a shallow groove. There is no definite nuchal organ, that is, no pocket-like invagination of the dorsal epithelium, such as is present in late post-larval and in adult examples of *Arenicola*. The next segment, which is also without chaetae, is homologous with the achaetous body segment of *Arenicola* (p. 37). Following this are the chaetiferous segments and the bluntly conical pygidium. The number of chaetiferous segments depends on the stage of growth attained. The largest number observed is fifty-one.

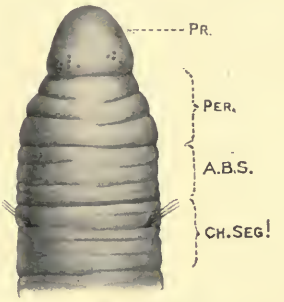

Fig. 59.—*B. vincenti.* Anterior end, dorsal aspect; PR. Prostomium, bearing groups of eyes; PER. Peristomium; A.B.S. Achaetous body-segment, CH.SEG.1. First chaetiferous segment. × 50.

Fig. 60.—*B. vincenti.* The chaetae of one of the posterior notopodia, in their natural position with regard to each other.

Each chaetiferous segment bears notopodial chaetae and neuropodial crotchets. The notopodia and neuropodia of all the preserved specimens are only slightly elevated above the rest of the body wall. The neuropodia are short, being much shorter than those of post-larval ecaudate *Arenicola* (*cf.* Pl. XI, Figs. 33, 35).

The annulation of the anterior and middle segments is much less definite, and the number of annuli per segment less constant than in *Arenicola*. In the larger specimens the segments from the third or fourth to nearly the thirtieth are divided into four to seven [1] rings. The last twelve to twenty segments are generally bi-annulate, the larger anterior ring bearing the chaetae and the smaller posterior one the gills (Pl. XI, Fig. 33). This condition was evidently presented also by Langerhans' specimens (see his Fig. 21 *g*), and it seems to be sufficiently constant to be cited as one of the diagnostic features of this worm.

CHAETAE.—Langerhans observed the presence of two kinds of notopodial chaetae, which he figured, but not very accurately.

[1] Some of these may not be true annuli, but may be due to folding of the body-wall brought about by contraction of its muscles.

They are not so markedly different as his figures imply. In each notopodium (Fig. 60) there are from two to four, occasionally five, straight or slightly curved chaetae of the type shown in Fig. 62 B, and a similar number of chaetae, each of which is bent so that the

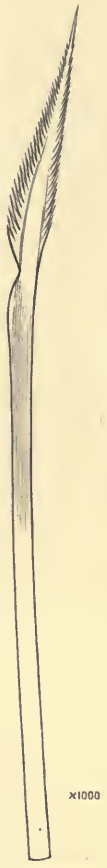

Fig. 61.—*B. vincenti* juv. (" *Clymenides incertus* "). Notopodial chaeta.

Fig. 62.—*B. vincenti*. The distal portions—in each case about three-fifths—of three notopodial chaetae. B, C. Typical adult chaetae; B is drawn in optical section; A, transitional form, intermediate between those shown in Fig. 61 and Fig. 62 B.

distal third or fourth makes with the proximal part an angle of about 150° (Fig. 62 C). Both these kinds of chaetae are cylindrical proximally, but beyond the middle of their length they become limbate (*cf.* Fig. 62 A). The limbate region merges into the tapering terminal

portion, which bears fine spinulations. The laminae of the chaeta are not entire at their margin, but are broken up, from the edge inwards, into fine, closely set teeth. The figures represent this part of the chaeta as seen in optical section. In some cases this region of the chaeta appears to be almost enveloped with the fine teeth, and the terminal part is invariably covered with them. In some specimens the two kinds of chaetae tend to merge into one another, and should probably be regarded as different facies of the same type. A notopodial chaeta of "*Clymenides incertus*," having a broader distal region and a well-marked constriction near the origin of the lamina on one side, is shown in Fig. 61. Fig. 62 A represents a transitional form, intermediate between the young chaeta of Fig. 61 and the adult chaeta of Fig. 62 B.

The neuropodial crotchets have the same general form as those of *Arenicola*, but the tip of the rostrum is very sharp (Fig. 64). The crotchets in each neuropodium are always few in number, they appear never to exceed nine or ten, and there are only two or three in the first two and last segments.

Fig. 63.—*B. vincenti* juv. ("*Clymenides incertus*"). Neuropodial crotchet.

Fig. 64.—*B. vincenti*, adult. Neuropodial crotchet.

Fig. 65.—*B. vincenti* juv. ("*Clymenides incertus*"). Crotchet from one of the posterior notopodia.

Prof. Mesnil stated that in his specimens of "*Clymenides incertus*," which had twenty, twenty-two and twenty-three chaetiferous segments respectively, each of the last six segments bore dorsally a crotchet, either alone or accompanied by a capillary chaeta. One of these crotchets, drawn from one of the original examples of "*C. incertus*,"

lent to the writer by Prof. Mesnil, is shown in Fig. 65. As in *Arenicola* (pp. 39–41) crotchets occur in the notopodia for a short period only; they are no longer present in two specimens of *B. vincenti*, 4 and 5 mm. long respectively, with twenty-seven segments.

Gills.—The gills of *B. vincenti* are of a much simpler type than those of *Arenicola*. Each consists of one, two or three, rarely four, finger-like filaments, not more than ·15 mm. long, each containing an extension of the coelom and a vascular loop. The position of the first gill is subject to variation: for instance, in the specimens examined by the writer, the first branchiate segment is the 18th, 19th, 19th, 20th, 21st and 21st respectively.[1] The succeeding segments, except perhaps the last or last two, are all branchiate.

Gills begin to arise about the time the worm has attained thirty segments, and then develop rapidly, for in a specimen with thirty-six segments, gills are present on the 19th to 34th inclusive.

Habitat.—Langerhans found *B. vincenti* living in small sand-covered tubes, among algae, on the rocks of the beach of Teneriffe. Prof. Mesnil collected his specimens in rock pools near Cape la Hague; the worms were inhabiting transparent mucous tubes, which were generally situated on the lower side of the encrusting calcareous alga *Lithothamnion*.

Colour.—Langerhans states that his specimens were brownish. Prof. Mesnil's first specimen was a clear grayish colour, but his later ones pale rose. Specimens preserved by him in formalin, and given to the writer, have a pale pink colour. The pigmentation is much less in amount than in specimens of *Arenicola ecaudata* of about the same size.

Internal Anatomy.—The coelom resembles, in its relations and proportions, that of an ecaudate *Arenicola*. The coelomic fluid contains numerous oval and spindle-shaped cells and the genital products. Septa are present at the anterior end of the first, third and fourth segments, and throughout the gill region. There are no septal pouches (Pl. XI, Fig. 32).

The alimentary canal is similar to that of *Arenicola*, except that the two oesophageal glands have a common duct.

[1] Langerhans records examples in which the first gill was borne on the 23rd and 24th segments respectively.

The lobate brain, oesophageal connectives, non-ganglionated nerve-cord (without giant fibres), and eyes are similar to those of a young *Arenicola*. Statocysts are absent.

The earlier statements regarding the nephridia of *B. vincenti* give the impression that there is considerable variation in the number of these organs. Prof. Mesnil (1897) referred to the presence of pigmented segmental organs in the 5th, 6th, 7th and 8th chaetiferous segments, and, in 1898, stated that four or five pairs were present; Prof. Fauvel attributed three to five pairs of nephridia to this worm, but Drs. Gamble and Ashworth found only two pairs, opening on the fifth and sixth segments. The writer has examined five specimens in regard to their nephridia, and in all of them only two nephridiopores could be seen, situated immediately *ventral* and posterior to the fifth and sixth neuropodia. By means of serial sections of two specimens and by dissection of another it has

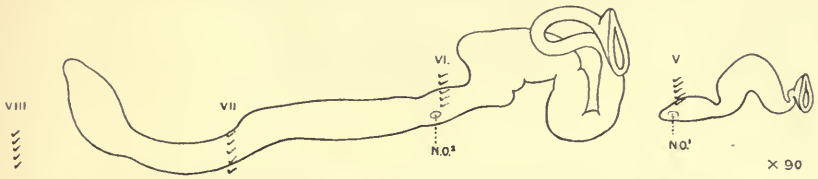

Fig. 66.—*B. vincenti*. Diagram of the nephridia of the left side, seen from the inner (median) aspect. The crotchets of the fifth, sixth, seventh, and eighth neuropodia (V, VI, VII, VIII), and the external openings (N.O¹, N.O²) of the first and second nephridia[1] are indicated.

been proved definitely that only two pairs of nephridia are present but the second is continued backwards, beyond its pore, as far as the eighth or ninth neuropodium, where it ends blindly (Fig. 66).

The gonads are situated on the coelomic epithelium, especially of the oblique muscles and septa. All the specimens examined by the writer were hermaphrodite. The oöcytes fall into the coelomic fluid at an early phase of growth; their later growth-phases are found chiefly in the posterior segments, the coelomic cavities of which, in mature specimens, are practically filled with large oöcytes (Fig. 67). When fully mature the eggs are, according to Prof. Mesnil, milk-white and about ·3 mm. long and ·2 mm. broad. They are thus considerably larger than those of any species of *Arenicola*, and taking into account the sizes of the parent worms, the eggs of *Branchio-*

[1] The funnels of the nephridia, which are small and difficult to investigate in preserved material, are apparently simple, but their structure can be determined satisfactorily only in living specimens.

maldane are relatively very large. A mature specimen of *Arenicola* may contain several or many thousands of full-grown oöcytes, but a mature specimen of *B. vincenti* contains comparatively few—about 120 were found in one specimen. The eggs of *B. vincenti* escape by rupture of the body-wall in one or more of the posterior segments.

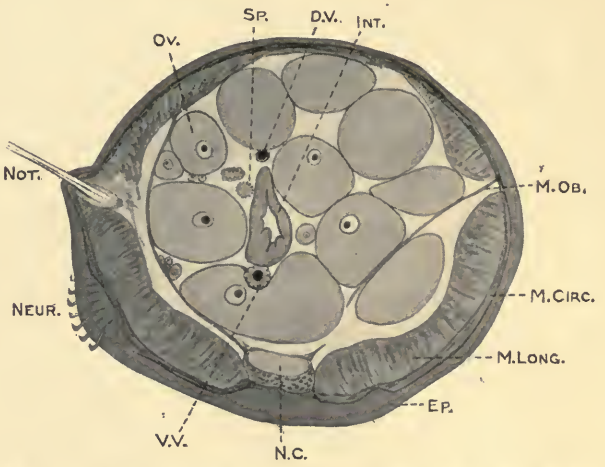

Fig. 67.—*B. vincenti.* Transverse section through the fortieth segment. D.V. Dorsal blood-vessel; EP. Epidermis; INT. Intestine; M.CIRC. Circular muscles; M.LONG. Longitudinal muscles; M.OB. Oblique muscle; N.C. Nerve-cord; NEUR. Neuropodium; NOT. Notopodium; OV Egg (oöcyte); SP. Mass of spermatocytes; V.V. Ventral blood-vessel. × 110.

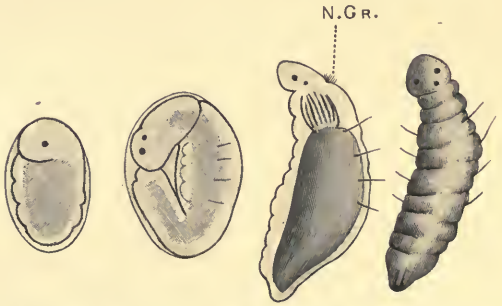

Fig. 68.—*B. vincenti.* Young stages of development (after Mesnil, 1898); N.GR. Nuchal groove.

PERIOD OF MATURITY, DEVELOPMENT. — Mature examples of *B. vincenti* have been recorded only by Prof. Mesnil, who collected them at St. Martin in August and September, 1898. The whitish eggs were found around the tubes which the worms inhabited.

To Prof. Mesnil we owe also the only observations on the develop-

ment of this worm (Fig. 68). He states that the "embryo" remains in the egg-membrane up to an advanced stage of development, finally becoming strongly flexed. When it becomes free, the young worm has two pairs of eyes and several segments, of which the third, fourth, fifth and sixth bear dorsal capillary chaetae, but not crotchets. Cilia were not visible except at the posterior dorsal margin of the prostomium, that is, in the nuchal groove.

Through the courtesy of Prof. Mesnil the writer has been enabled to examine the three original specimens of "*Clymenides incertus*," which are about 2·5 mm. long, and he has no hesitation in stating that they are young phases of *B. vincenti*. A comparison of the capillary chaetae (Figs. 61, 62) of "*C. incertus*" with those of *B. vincenti* shows that they are all growth forms of the same type of chaeta, and the neuropodial crotchets (Figs. 63, 64) present identical characters. Other important points of agreement are afforded by the prostomium, the segmentation of the body and the absence of statocysts.

Systematic Position.—*Branchiomaldane* is more nearly related to *Arenicola* than to any other Polychaete and must be included in the family Arenicolidae, but the writer is of opinion that the union of the two genera *Branchiomaldane* and *Arenicola*, recommended by Prof. Fauvel, is not advisable. Prof. Fauvel has pointed out that *Branchiomaldane* presents several points of resemblance to a young *A. ecaudata*, but it may be noted in this connection that, as these worms live under practically identical conditions, some of the similarities may be due to convergence. Further, some of the resemblances cited by Prof. Fauvel are not so close as they were believed to be; compare, for instance, the nephridia and the position of the gills in *Branchiomaldane* and *Arenicola*. It is also worthy of note that in the most nearly related species of *Arenicola*, namely, *A. ecaudata* and *A. branchialis*, there are well developed statocysts and septal pouches, which are wanting in *Branchiomaldane*. Other important characters presented by *Branchiomaldane*—the occurrence of hermaphroditism, the extensive distribution of the reproductive organs on the oblique muscles and septa, the production of comparatively few, large and plentifully-yolked eggs, which do not give rise to free swimming ciliated larvae—are not paralleled in *Arenicola*. The striking differences in the branchiferous segments—which are bi-annulate in *Branchiomaldane*, the setae and gills being borne on successive annuli, while in *Arenicola* they are subdivided into five,

the largest of which is chaetiferous and branchiferous—are, however, alone sufficient, in the writer's opinion, to render necessary the maintenance of the two genera.

While *Branchiomaldane* presents some primitive characters, for instance, a simple conical prostomium, and homonomy of its segments, there is considerable evidence of its having undergone secondary modification and retrogression. Its small size, the simple form of its gills, the absence or great reduction of certain sense organs (statocysts and nuchal organ), the reduction in the number of nephridia, its hermaphroditism, the large size of the eggs and the absence of a free-swimming larval stage—features in which *Branchiomaldane* departs from *Arenicola*—are probably to a large extent correlated with the much more sedentary life of the former.

The systematic position of *Branchiomaldane vincenti* may be summarised thus—it is an Arenicolid worm, most nearly related to the ecaudate species of *Arenicola*, to the young stages of which it presents some points of similarity, both in form and habits, but from which it differs in several important structural characters. Although their habits are at first similar, the species of *Arenicola* soon assume a more wandering mode of life, which they maintain henceforward, whereas *Branchiomaldane* remains sedentary, is, in fact, tubicolous, and exhibits certain retrogressive changes which are often associated with that mode of life.

Near Cherbourg . . . Ashworth Coll. 1912. 4. 9. 46.

THE INTER-RELATIONSHIPS OF THE MEMBERS OF THE FAMILY ARENICOLIDAE.

The presence of homonomous segments, as in the ecaudate species of *Arenicola*, is undoubtedly the primitive condition, while the differentiation of the worm into two regions, an anterior in which the segments bear parapodia and a posterior which has become achaetous, and in which the segments are feebly marked, as in the caudate species, is clearly secondary and is probably correlated with a more sedentary mode of life. Of the ecaudate species *A. ecaudata* possesses the greater number of segments, namely, about sixty, compared with about forty in *A. branchialis*, and the former may be regarded on this ground, as well as on account of its much larger number of nephridia, as more nearly retaining the original condition. The fact that *A. ecaudata* has, when complete, about

sixty segments, and that the definitive number of segments in *A. cristata* is also about sixty (seventeen chaetiferous and forty caudal), suggests that this may have been approximately the number present in the common ancestor of the genus.

A. ecaudata possesses the largest number of nephridia, namely, thirteen pairs, and probably, therefore, exhibits the nearest approach to the primitive condition; the other species do not possess normally more than five or six pairs, but that the series of nephridia in these species formerly extended further back is indicated by the occasional occurrence of nephridia in one to three segments behind that containing the last normal nephridium (see p. 82).

Well-developed statocysts are so characteristic a possession of the genus *Arenicola*, there being only one species—*pusilla*—in which these organs are absent, that it may be assumed they were present in the ancestral form. The statocysts have retained their primitive condition, as epidermal invaginations opening to the exterior, in *A. marina, assimilis* and *glacialis;* in the other species they have become transformed into closed vesicles, either with numerous statoliths as in the ecaudate species, or with a single endogenous statolith as in *A. loveni* and *cristata*, which exhibit the most specialised condition of the organ. The absence of statocysts in *A. pusilla* appears to be a secondary, and not a primary condition.

The prostomium, which in all species of *Arenicola* is reduced to small dimensions (a condition no doubt associated with the semi-sedentary mode of life), has the simplest form in the ecaudate species, in which it has retained its primitive relations, being situated anterior to the peristomium and partially overhanging the mouth. In the caudate species the prostomium is retractile into the nuchal groove and then no longer exhibits the typical relations.

The primitive characters are not all concentrated in one species of *Arenicola*, but it seems clear that a greater number of them have been preserved in the ecaudate species, and especially in *A. ecaudata*, the statocysts of which have, however, advanced some distance on the way of specialisation. In *A. branchialis* the segments and nephridia have both been diminished in number, probably correlatively, and the gonads are much smaller, but otherwise this species is similar to *A. ecaudata*.

The caudate species are divisible into two divergent series, one—including *A. marina, glacialis, loveni* and *cristata*—possessing elongate neuropodia, septal pouches and a single pair of oesophageal glands, the other—comprising *A. assimilis* and *pusilla*—in which the

neuropodia are short, septal pouches are absent, and there are several pairs of oesophageal caeca. Of the caudate species, *A. marina* and *A. assimilis* present fewest modifications and stand near the bases of origin of the two series. Nearly related to *A. marina* is *A. glacialis*, their close affinity being indicated by the similarity of their neuropodia, chaetae, oesophageal glands, septal pouches, nephridia and statoliths; the gills and prostomium of *A. glacialis* also more nearly resemble those of *A. marina* than of any other species. The chief difference between these two species is that in *A. glacialis* the chaetiferous segments and gills are reduced in number.

The two species *A. loveni* and *A. cristata* have apparently sprung from the same stem, for in both the neuropodia are long, the gills highly pinnate, the septal pouches large, and the statocysts closed and

each containing only a single large statolith. Further indication of their affinity is afforded by the similar form of their prostomia; while, in the character of its chaetae, *A. loveni* presents a closer approach to *A. cristata* than to any other species. *A. loveni* exhibits considerable specialisation in its extraordinary septal pouches and its notopodial chaetae, while *A. cristata* has undergone modification in another direction, namely, reduction in the number of its chaetiferous segments and gills. The two species *A. loveni* and *A. cristata* are clearly more nearly related to each other than either is to *A. marina*.

A. assimilis and *A. pusilla* diverge from the rest of the species in several striking features (p. 157) and have developed along an independent line. *A. assimilis* has primitive statocysts, and its prostomium is little modified, being not much dissimilar to that of

A. marina. The close resemblance of the chaetae of *A. assimilis* and *A. marina* is also noteworthy. *A. assimilis* is probably an old species, perhaps as old, or nearly so, as *A. marina*. *A. pusilla* has undergone considerable specialisation, for instance, in its crotchets, in the high degree of development of its prostomium, and in the absence of statocysts. In other respects *A. pusilla* presents characters similar to *A. assimilis* and is clearly derived from the same stem.

Branchiomaldane, which is most nearly related to the ecaudate species of *Arenicola* (see pp. 155, 156), appears to have branched off near the base of the primitive stem of the family, and, while retaining some primitive characters, has undergone certain retrogressive changes associated with its tubicolous mode of life.

The relationships discussed above are indicated in the diagram given on p. 158.

THE AFFINITIES OF THE ARENICOLIDAE.

The first satisfactory suggestion respecting the relationship of *Arenicola*[1] was that of Blainville (1828), who, noticing that the Téléthuses and the Maldanies agree in possessing both subulate chaetae and crotchets, placed these two families in one order, although one contains branchiate and the other non-branchiate worms (see p. 15). It is difficult to understand on what grounds Milne Edwards (1838) united *Arenicola* and *Chaetopterus* in the tribe Arenicolides, nor is it evident why he and, later, Oersted (1843), suggested the affinity of *Arenicola* with the Ariciae. The schema given by Grube in his classical paper (1850) shows that he regarded the Telethusa[2] as related on the one hand to the Maldania and on the other to *Scalibregma* and *Eumenia*, a view which subsequent work has confirmed. Dr. Levinsen (1883) ranged the Telethusae with the Scalibregmidae, but united these with the Amphinomidae to form a sub-order Amphinomiformia. The Amphinomidae differ from *Arenicola* in so many important features that there is no basis in support of the association suggested.

Prof. Benham placed the Arenicolidae in the sub-order Scoleciformia along with the families Opheliidae, Maldanidae, Scalibregmidae, Chlorhaemidae and Sternaspidae, and Prof. Hatschek included the

[1] *Arenicola marina* was the only species then known.

[2] In which family Grube at first included *Arenicola* and *Dasybranchus*, but later (1862) he removed the latter genus to a new family Capitellacea.

Arenicolidae, Cirratulidae, Capitellidae and Maldanidae in the sub-order Drilomorpha. On passing in review the characters of these families it is at once seen that the Sternaspidae are far removed from the Arenicolidae by the peculiar arrangement of their gills, chaetae and gonad, by the presence of ventral shields, genital ducts, a coiled alimentary canal without oesophageal glands, and only a single pair of nephridia, and by the absence of septa. The anatomy of the Chlorhaemidae, which is, however, only imperfectly known, affords no evidence of relationship between this family and the Arenicolidae; there are so many pronounced structural differences—for instance, in the nature of the prostomium, gills, chaetae, nerve-cord, the arrangement of the septa and the nephridia—that it may be concluded these are not allied families. The Cirratulidae are also separated from the Arenicolidae by a series of striking differences, for instance, in their chaetae, gills, nephridia and prostomium. The Capitellidae, though having some points of external resemblance to the Arenicolidae, exhibit such differences that it seems clear these families are not nearly related; consider, for example, the nephridia and genital funnels of Capitellids, the different arrangement of their parapodia, the presence of genital chaetae and hooded crotchets, the form of the gills (when present), the regularly septate coelom, the ganglionated nerve-cord, and the absence of blood-vessels and oesophageal glands.

There are several characters common to the families Arenicolidae, Scalibregmidae and Opheliidae, which are probably due to their similar mode of life, the members of these families being limivorous. They have a spacious coelom, subdivided anteriorly by septa but non-septate in the middle portion of the animal, the alimentary canal consists of an eversible pharynx, followed by an oesophagus (bearing one or more pairs of glandular caeca), a dilated "stomach" and a straight intestine. In addition to these features the Scalibregmidae[1] agree with the Arenicolidae also in the subdivision of their segments into annuli, in the sculpturing of the skin, and in the presence in *Scalibregma* and *Eumenia* of branched gills of a type similar to those of *Arenicola*. The brain and the non-ganglionated cord of *Scalibregma* are similar to those of the caudate species of *Arenicola*. But there are several characters in which the Scalibregmidae differ sharply from the Arenicolidae; for instance, the two rami of the parapodia of the former are practically identical in form, there are no crotchets,

[1] See J. H. Ashworth, "The Anatomy of *Scalibregma inflatum* Rathke," in Q. J. Micr. Sci., xlv (1901), p. 237.

but characteristic furcate chaetae are present, along with capillary chaetae, in both rami of the parapodium; in some of the Scalibregmidae the parapodia form laminate appendages bearing dorsal and ventral cirri; the gills do not extend, in the Scalibregmidae, backwards beyond the fifth or sixth segment, the heart is a median dilatation on the dorsal vessel, the nephridia are numerous and minute, and complex lateral sense organs are generally present, but statocysts and eyes are absent.

Besides the features mentioned above (p. 160) as common to the three limivorous families, the Opheliidae[1] agree with the Arenicolidae in possessing nephridia of a similar type, but differ in several important respects, for instance, in the form of the prostomium, in having a ganglionated nerve-cord, in the nature of their gills which, when present, are cirriform, in the presence of anal cirri and a dorsal heart, in the absence of septa in the posterior region, and in the absence of crotchets and statocysts.

The Arenicolidae present clear affinities with the Maldanidae.[2] The head of some of the Maldanids, *e.g. Praxillura*, is similar in form to that of the ecaudate species of *Arenicola*, but the cephalic plate present in many Maldanids has no counterpart in *Arenicola*, while, conversely, a trilobate prostomium like that of the caudate species of *Arenicola* does not occur in the Maldanids. The two families agree in the form of their parapodia and chaetae, capillary chaetae and crotchets being present in both. The notopodial chaetae of Maldanids closely resemble those of Arenicolidae, especially those of young examples, and the crotchets of some Maldanids, *e.g. Petaloproctus*, might easily be mistaken for those of *Arenicola*. The brain and non-ganglionated nerve-cord, the nephridia and gonads of Maldanids are of a type similar to those of the Arenicolidae. The Maldanids differ from the Arenicolidae in having paired nuchal organs, and elongate and non-annulate segments, in lacking gills,[3] oesophageal caeca, hearts and statocysts,[4] and in the specialisation of the anal segment. *Branchiomaldane* has been regarded, on

[1] See W. Kükenthal, Jenaische Zeits., xx (1887), p. 511; and M. Philippson, Zool. Anz., xxii (1899), p. 417.

[2] See I. Arwidsson, Zool. Jahrb. Abt. Syst., Suppl. ix (1907), p. 1.

[3] The Maldanid *Jchnstonia*, has, on the six pre-anal segments, numerous, short, simple elevations, which serve as respiratory organs.

[4] The Arenicolidae are regarded as having been derived from an ancestor having statocysts. These organs are absent in *Arenicola pusilla* and *Branchiomaldane vincenti*, which, however, exhibit marked specialisation in several other respects.

account of its tubicolous habits, and of the feeble development of its gills and the absence of statocysts, as forming a link between the two families; but, as already shown (p. 155), there is no doubt that this genus is a member of the family Arenicolidae, though its habits are similar to those of Maldanids.

A consideration of the characters of the Arenicolidae shows that this family has clear affinities with the Maldanidae, and also, but in less degree, with the Scalibregmidae, and in still less degree with the Opheliidae.

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Synonyms are printed in italics.

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Ventral nerve-cord of *Arenicola*, 66.
Vermes, 2–9; distinguished from "Insecta," 9.
vincenti (*Branchiomaldane*), 147–159.

Willis, 4.
Willughby, 5, 91.
Wotton, 2.

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DESCRIPTION OF PLATES I–XV

LIST OF REFERENCE LETTERS

A.B.S. . . Achaetous body-segment.
Acic. . . Aciculum.
Bl.V. . . Blood-vessel.
Br.[1] . . First gill.
Ch.Seg.[1] . First chaetiferous segment.
D. . . . Diatom (as statolith).
D.V. . . Dorsal blood-vessel.
Ep. . . . Epidermis.
Gon. . . Gonad.
Gon.V. . . Gonadial blood-vessel.
H. . . . Heart.
M. . . . Muscle-band.
M.Circ., *M.Long.* } Circular and longitudinal muscles of body-wall.
M.Gr. . . Metastomial groove.
Mo. . . Mouth.
N.C. . . Nerve-cord.
Neur . . Neuropodium.
Neur.[1] . . First neuropodium.
N.O. . . External opening of nephridium.
N.O.[1] . . External opening of first nephridium.
Not. . . Notopodium.
Not.[1] . . First notopodium.
Not.Pr., *Not.Retr.* } Protractor and retractor muscles of notopodium.
Not.S. . . Notopodial chaetal sac.
Nph.[1] . . First nephridium.
Nph.F.D. . Dorsal lip of nephridia funnel.
Nph.F.V. . Ventral lip of nephridial funnel.
N.Sh. . . Nervous sheath of statocyst.
N.St. . . Nerve to statocyst.
Nuc.Gr. . Nuchal groove.
Œ. . . . Oesophagus.
Œ.Conn. . Oesophageal connective.
Œ.Gl. . . Oesophageal gland.
P. . . . Pit (possibly sensory).
Per. . . Peristomium.
Prost., or *Pr.* } Prostomium.
S^1, S^2, S^3 . First, second and third septa.
S.P. . . Septal pouch.
S.P.O. . . Opening of septal pouch into coelom.
St. . . . Statocyst.
Sth. . . Stomach.
St.O. . . Opening of statocyst to exterior.
Stom. . . Stomodaeum.
St.T. . . Tube from statocyst to exterior.
Tent. . . Tentacle.
Ves. . . Vesicle, or bladder, of nephridium.

PLATE I.

Arenicola marina (Linnaeus). Light- and dark-coloured examples, taken, at the same time, from the beach at Musselburgh, Firth of Forth.

Fig. 1.—A typical light-coloured example. The buccal mass and pharynx are protruded.

Fig. 2.—Anterior end of a similar specimen; dorsal aspect.

Fig. 3.—A dark-coloured example.

Fig. 4.—Anterior end of a similar specimen, with buccal mass and pharynx protruded; dorsal aspect.

PLATE II.

Fig. 5.—*A. branchialis* Audouin and Edwards (*A. grubii* Claparède), from Plymouth.

Fig. 6.—*A. branchialis*, anterior end, dorsal aspect. The first notopodium was wanting, a condition not uncommon in this species.

Fig. 7.—*A. ccaudata* Johnston, from Plymouth. .

Fig. 8.—*A. ccaudata*, anterior end, dorsal aspect.

PLATE III.

Fig. 9.—*A. loveni* Kinberg, from Saldanha Bay, Cape Colony.

PLATE IV.

Figs. 10, 11.—Dissections of the anterior portions of *A. marina* (Linnaeus) (Fig. 10), from Musselburgh, and *A. loveni* Kinberg (Fig. 11), from Saldanha Bay. The specimens were opened along the mid-dorsal line. Compare their septal pouches and nephridia. The septal pouches of the specimen of *A. marina* were dilated; they are usually rather smaller than they are here represented.

PLATE V.

A. cristata Stimpson.

Fig. 12.—A specimen from Naples, with full number of tail-segments. Neuropodia were absent in the first two chaetiferous segments.

Fig. 13.—Last chaetiferous segment and tail (consisting of only eight segments) of a specimen, from Wood's Holl, Mass., to show the caudal processes, one of which—on the first tail-segment—is branched and gill-like.

PLATE VI.

Fig. 14.—*A. glacialis* Murdoch. Type specimen. Note the presence of an eighteenth neuropodium. The buccal mass and pharynx are fully protruded. The tail is, in the specimen, strongly contracted; it has been represented in the figure in a condition of more normal extension.

PLATE VII.

Fig. 15.—*A. pusilla* Quatrefages (*A. claparedii* Levinsen), from Naples.

Fig. 16.—*A. assimilis* Ehlers, from Uschuaia, Beagle Channel. Co-type from Naturhistorisches Museum, Hamburg.

PLATE VIII.

Fig. 17.—*A. cristata* Stimpson, from Naples. Dissection of the anterior portion. The specimen was opened along the mid-dorsal line. Note especially the nephridia, the small oesophageal glands, and the septal pouches.

Fig. 18.—*A. pusilla* Quatrefages (*A. claparedii* Levinsen), from Naples. Dissection of the anterior portion. The specimen was opened along the mid-dorsal line. Note especially the nephridia, the oesophageal glands (five pairs), and the absence of septal pouches.

PLATE IX.

Fig. 19.—*A. ecaudata* Johnston, from Plymouth (August, 1910). Dissection of the anterior portion of a mature male example. The specimen was opened along the mid-dorsal line. The portion of the oesophagus between the glands and the hearts is unusually extended and dilated with food. The testis on the fifth left nephridium is produced into two thin outgrowths, one overlying the other, and the testis borne by the third right nephridium presents a similar condition; each of the other testes bears only one such outgrowth (see Pl. XV. Fig. 53).

Fig. 20.—*A. branchialis* Audouin and Edwards (*A. grubii* Claparède), from Plymouth. Dissection of the anterior portion of a mature specimen; the reproductive organs are small (see Pl. XV, Fig. 51).

PLATE X.

Figs. 21–25.—*A. pusilla* Quatrefages (*A. claparedii* Levinsen).

Fig. 21.—Larva, about thirty hours after fertilisation of the egg; ventral aspect (see p. 74).

Fig. 22.—Larva, dorsal aspect; about forty hours older than the preceding, and on the point of forcing its way out of the vitelline membrane, through the thin area in the upper part of the same.

Fig. 23.—Larva, one day after hatching; dorsal aspect. The larva was slightly compressed under the cover-glass, and therefore appears a little too broad. The first notopodial chaetae have been formed.

Fig. 24.—Larva, twelve days after hatching; right aspect. The middle portion of the gut still contains yolk. Note the two kinds of notopodial chaetae and the crotchets.

Fig. 21–24 were drawn, in Naples, from living larvae, which had developed from eggs fertilised artificially.

Fig. 25.—One of the eyes of the larva shown in the preceding figure. Note the cup-shaped group of pigment-spherules, and the lens (see p. 70).

Figs. 26–28.—*A. marina* (Linnaeus), from Plymouth (see p. 77).

Fig. 26.—Post-larval example, 4·7 mm. long, in its mucous tube, as found in the plankton.

Fig. 27.—Post-larval example, about 6 mm. long; anterior end, dorsal aspect.

Fig. 28.—Left aspect of the anterior portion of a stained and cleared post-larval specimen, 4·5 mm. long.

Fig. 29.—*A. assimilis* Ehlers var. *affinis* Ashworth. Left aspect of the anterior portion of a stained and cleared post-larval specimen, 11 mm. long, from the Falkland Islands (see p. 80).

Fig. 30.—*A. cristata* Stimpson. Post-larval specimen, 6 mm. long, from Wood's Holl, Mass., showing the full number of tail-segments and the incipient gills (see p. 79). The neuropodial crotchets are indicated by vertical series of white dots.

PLATE XI.

Figs. 31–33.—*Branchiomaldane vincenti* Langerhans, from near Cherbourg.

Fig. 31.—Adult, but rather contracted, specimen, 8 mm. long (see p. 148).

Fig. 32.—Anterior portion of an adult specimen, about 10 mm. long, stained and cleared (see p. 152).

Fig. 33.—Posterior portion of a well-extended specimen, 10·5 mm. long, showing the characteristic bi-annulate segments, in which the anterior ring is chaetiferous and the posterior branchiferous.

Figs. 34, 35.—*A. ecaudata* Johnston, from near Cherbourg.

Fig. 34.—Young, abranchiate post-larval specimen, 4·6 mm. long (see p. 80).

Fig. 35.—Fifteenth to twentieth segments of a late post-larval stage, 11 mm. long, seen from the left side; showing the gills on the sixteenth and succeeding segments. Note that the gills are situated on the respective chaetiferous annuli (*cf.* Fig. 33), and that the neuropodia are much longer than those of *Branchiomaldane* (*cf.* Figs. 31, 33).

PLATE XII.

Figs. 36–38.—*Nereis cultrifera* Grube, from Plymouth.

Figs. 36, 37.—Dorsal (Fig. 36) and ventral (Fig. 37) views of the anterior end, to show the pre-oral prostomium (Pr.), with its eyes, tentacles and palps, the peristomium (Per.), with its cirri and the mouth, and the first two chaetiferous segments, with their parapodia.

Fig. 38.—Parapodium or "foot," consisting of a basal piece and two distal, lobate processes—the notopodium and neuropodium—each of which bears a sensory cirrus, a bundle of chaetae (the tips of which project from the mouth of the sac in which the chaetae were formed), and an aciculum, which serves as an internal skeleton.

Figs. 39, 40.—*A. marina* (Linnaeus).

Fig. 39.—Transverse section, passing through a parapodium, showing the notopodial chaetal sac, with its chaetae and its protractor and retractor muscles, and the neuropodial chaetal sac, with its crotchets (see pp. 34, 35).

Fig. 40.—Anterior end, dorsal aspect; showing the buccal mass protruded, the prostomium, nuchal groove, metastomial groove, and the openings of the statocysts. From a specimen preserved with the anterior end fully distended.

PLATE XIII.

Figs. 41, 42.—*A. cristata* Stimpson (175 mm. long). The dorsal axis of the first gill (Fig. 41) and of the fifth gill (Fig. 42). Pinnate type of gill (see p. 58).

Fig. 43.—*A. marina* (Linnaeus), littoral form (120 mm. long), second left gill. Fruticose or bushy type of gill (see pp. 58, 59). Most of the gill-axes have been cut away near their origins.

Fig. 44.—*A. pusilla* Quatrefages (*A. claparedii* Levinsen), from California. A portion of the alimentary canal, at the junction of oesophagus and stomach, to show the multiple oesophageal glands (see p. 63). The posterior part of the oesophagus is contracted, and the glandular caeca form a cluster.

Fig. 45.—*A. assimilis* Ehlers, var. *affinis* Ashworth, from Table Bay, Cape Colony. A portion of the alimentary canal, at the junction of oesophagus and stomach, to show the multiple oesophageal glands. The posterior part of the oesophagus is unusually extended.

Fig. 46.—*A. marina* (Linnaeus). Dissection of the anterior end, from the dorsal surface; the buccal mass and pharynx have been cut away to show the prostomium, oesophageal connectives, statocysts and septal pouches.

PLATE XIV.

Fig. 47.—*A. marina* (Linnaeus). Section of the statocyst and the tube leading to the exterior. The statoliths are naked irregular bodies, chiefly quartz-grains; one (D) is a diatom (see p. 67).

Fig. 48.—*A. marina* (Linnaeus). Fourth left nephridium, dorsal aspect. The ventral lip (Nph. F.V.) of the funnel is seen through the dorsal one (see p. 71).

Fig. 49.—*A. pusilla* Quatrefages (*A. claparedii* Levinsen). Ventral aspect of anterior portion of third left nephridium of a large specimen (160 mm. long.) from Unalaska; M. Band of muscle which binds the funnel to the body-wall.

Fig. 50.—*A. assimilis* Ehlers. Ventral aspect of anterior portion of second right nephridium, showing that the ventral lip of the funnel is thrown into folds or frills (see p. 71).

PLATE XV.

Fig. 51.—*A. branchialis* Audouin and Edwards (*A. grubii* Claparède). Fourth left nephridium, dorsal aspect. The deeply-notched ventral lip (Nph. F.V.) of the funnel is seen through the dorsal one.

Fig. 52.—*A. ecaudata* Johnston. Female specimen from Plymouth; fifth right nephridium with mature ovary, dorsal aspect (see p. 73).

Fig. 53.—*A. ecaudata* Johnston. Male specimen, from Plymouth; tenth left nephridium, with mature testis, dorsal aspect (see p. 73). The deeply notched ventral lip (Nph. F.V.) of the funnel is seen through the dorsal one.

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Fig.1. x1½.

Fig.4. x2.

Fig.2. x3.

Fig.3. x1⅛.

Arenicola marina (Linnaeus)
Light and dark-coloured examples.

A.K Maxwell del. E.Wilson, Cambridge.

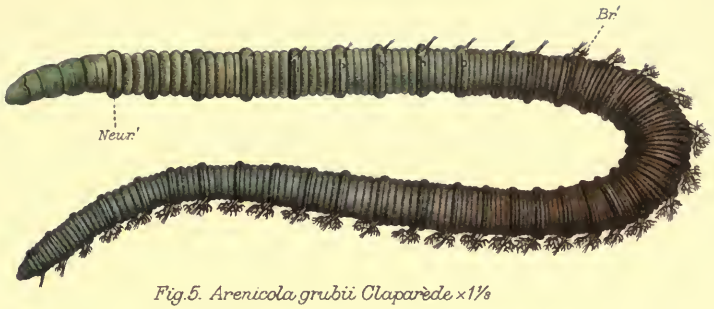


Fig.5. Arenicola grubii Claparède ×1⅛

Fig.6. A.grubii Clap.
x 3

Fig.8. A.ecaudata Johnst.
x 3

For *Arenicola grubii* Claparède, read *Arenicola branchialis* Audouin and Edwards (see pp. 141–3, and p. 143, footnote).

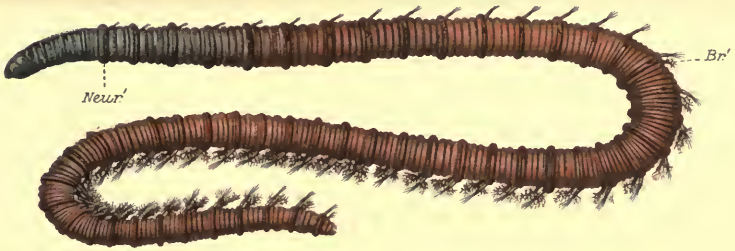


Fig.7. Arenicola ecaudata Johnston ×1⅛

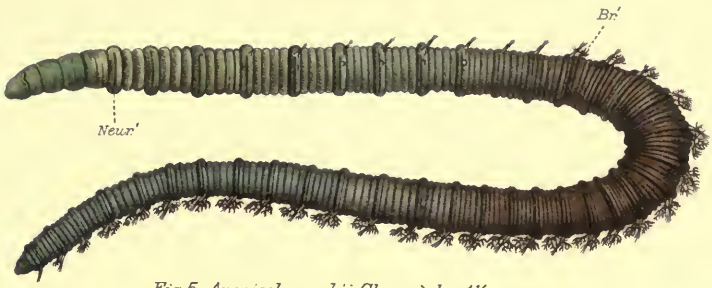


Fig.5. Arenicola grubii Claparède x1⅓

Fig.6. A.grubii Clap. x3

Fig.8. A.ecaudata Johnst. x3

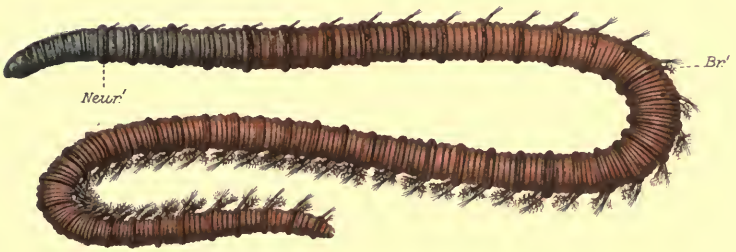


Fig.7. Arenicola ecaudata Johnston x1⅓

A.K.Maxwell, del. E Wilson, Cambridge.

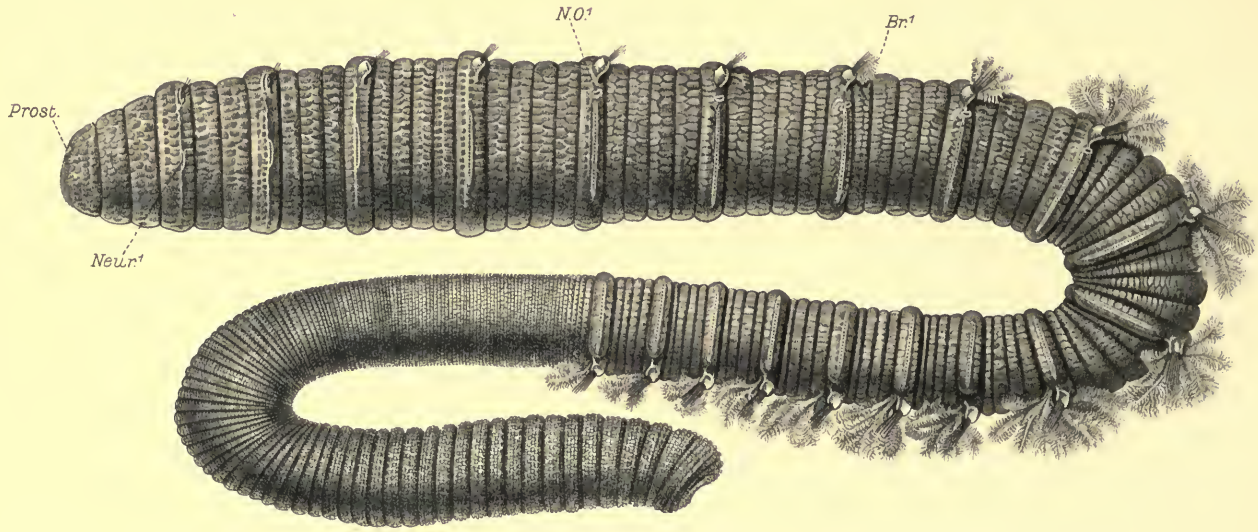


Fig. 9. Arenicola loveni Kinberg. x1.

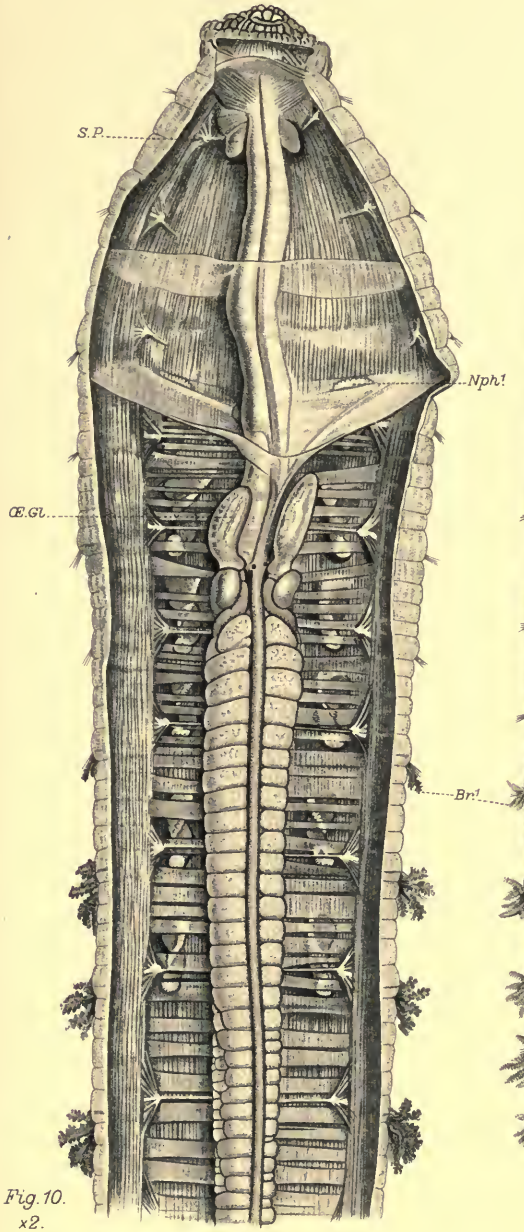


Fig. 10.
x2.

Arenicola marina (Linnaeus.)

A.K.Maxwell del.

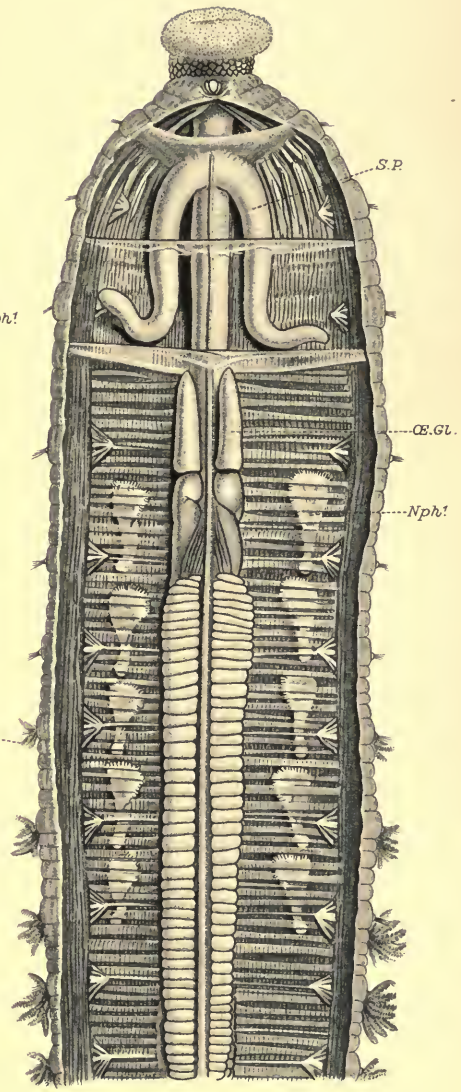


Fig. 11.
x1¼.

Arenicola loveni Kinberg.

E.Wilson, Cambridge.

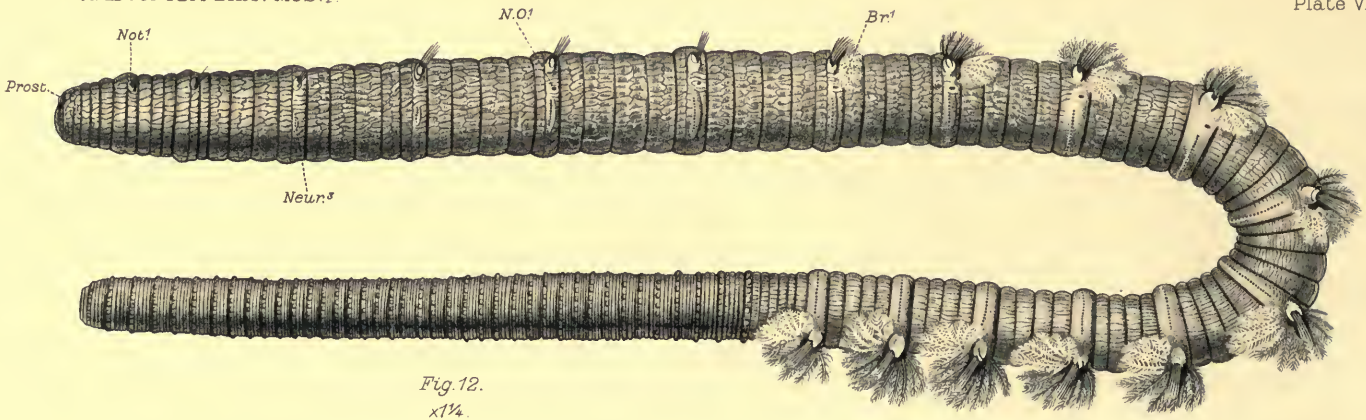


Fig. 12.
x1¼.

Fig. 13.
x2

Arenicola cristata Stimpson.

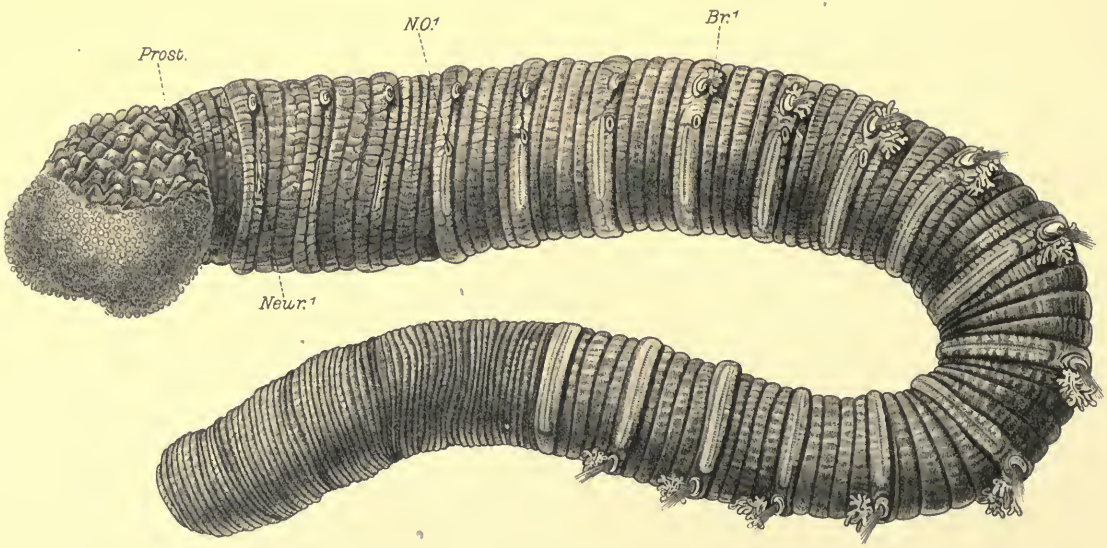


Fig. 14. Arenicola glacialis Murdoch.
Type specimen. x3.

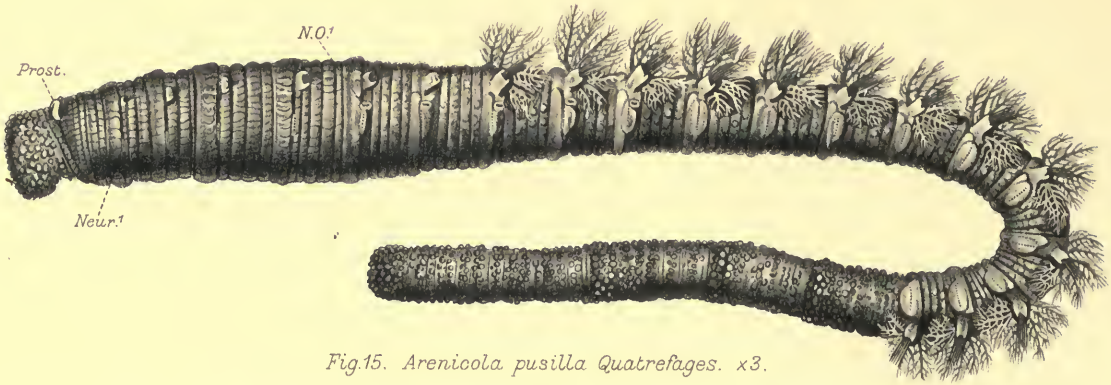


Fig.15. Arenicola pusilla Quatrefages. x3.

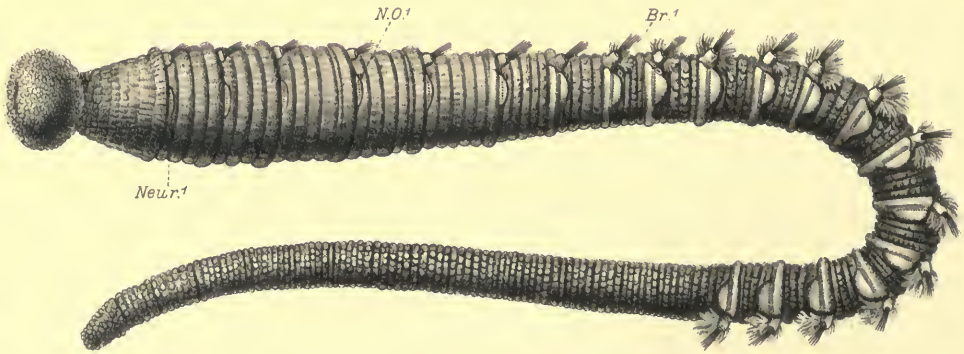


Fig.16. Arenicola assimilis Ehlers. x2.

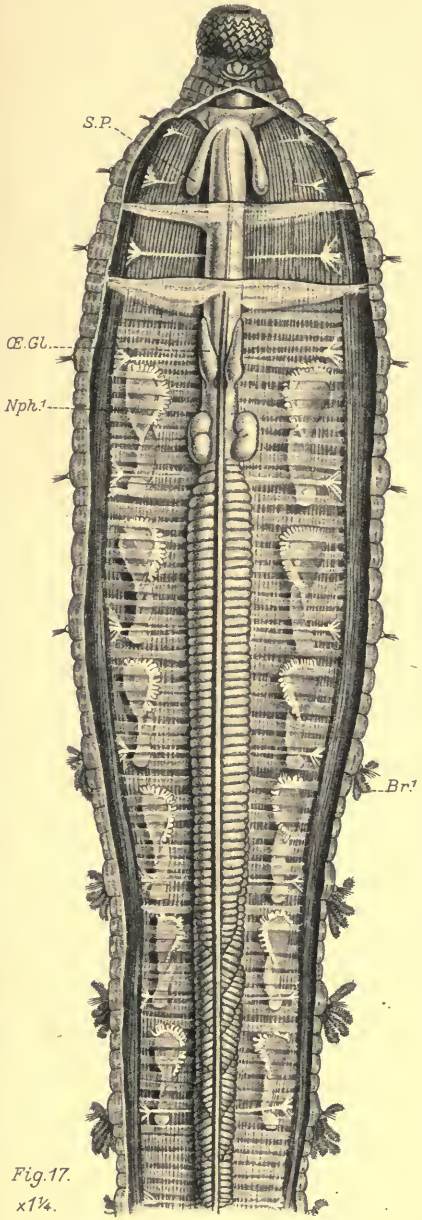


Fig. 17.
x1¼.

Arenicola cristata Stimpson.

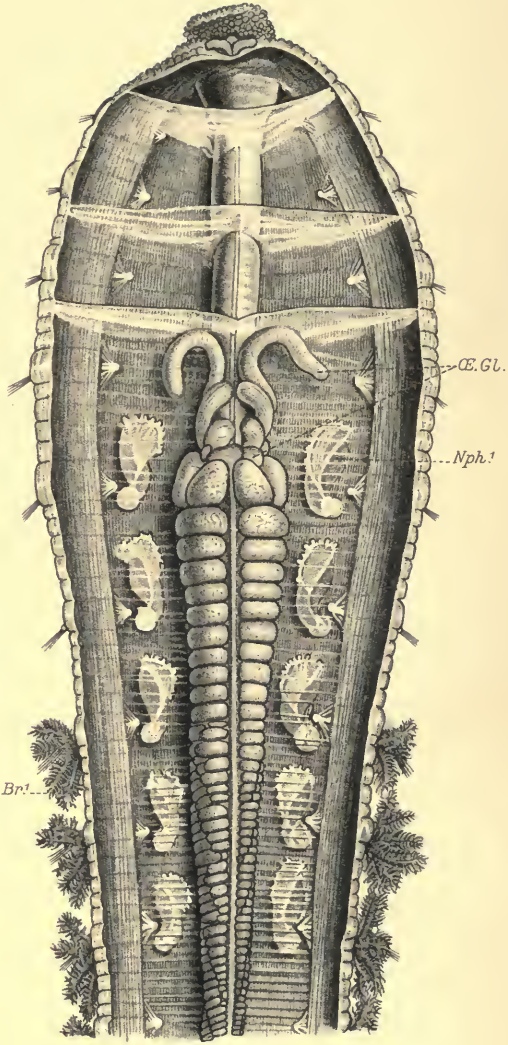


Fig. 18.
x4.

Arenicola pusilla Quatrefages.

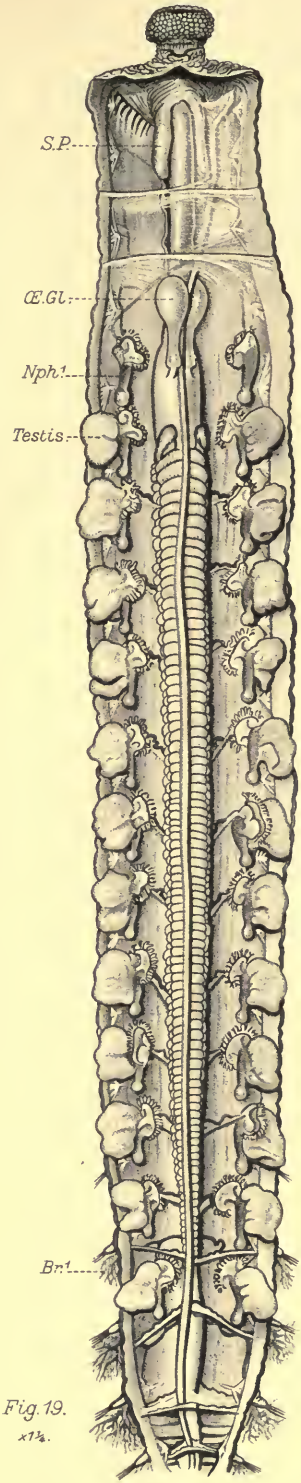


Fig. 19.
×1¼.

Arenicola ecaudata Johnston.
Male specimen.

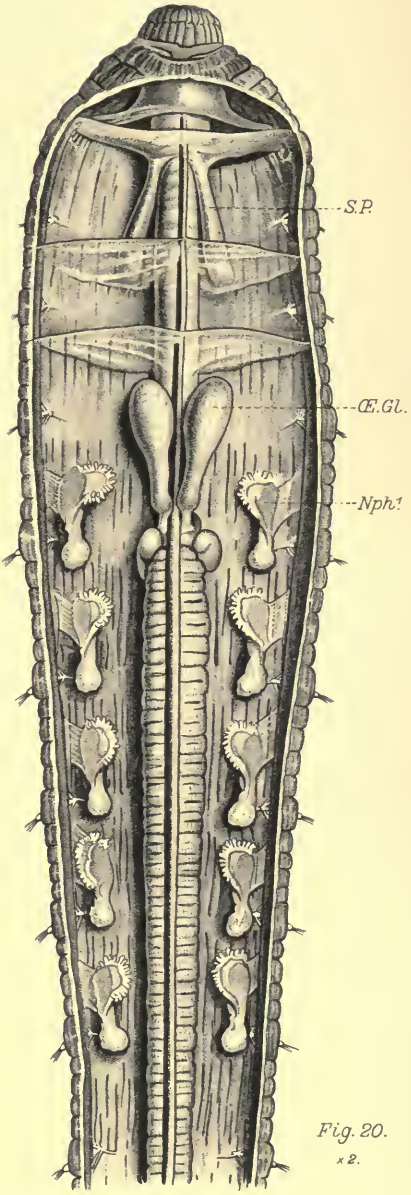
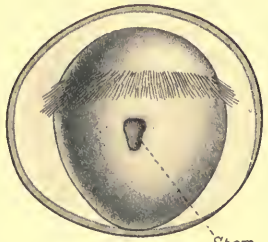


Fig. 20.
×2.

Arenicola branchialis.
Audouin & Edwards.

A.K.Maxwell del.
E.Wilson, Cambridge.



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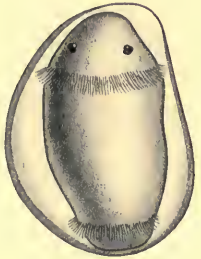

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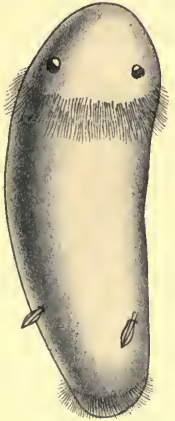

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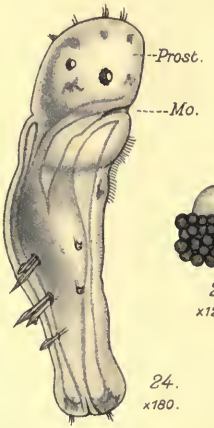

24. x180.

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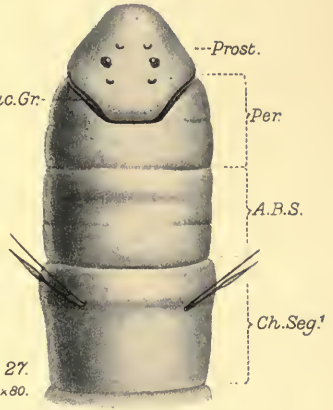

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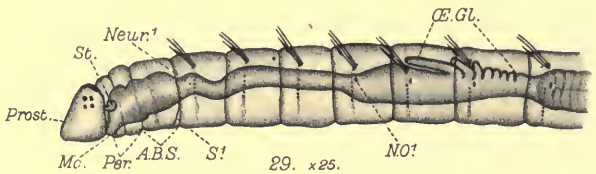

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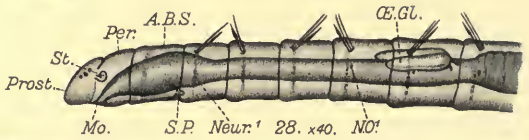

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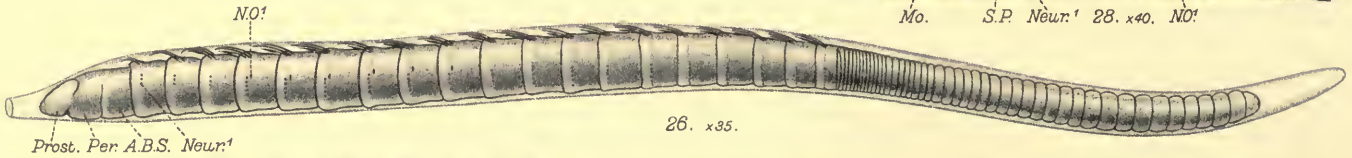

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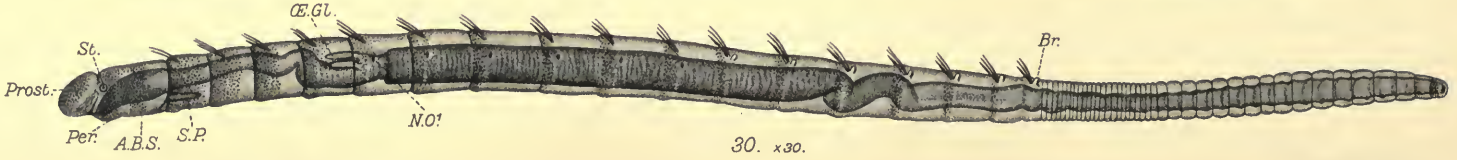
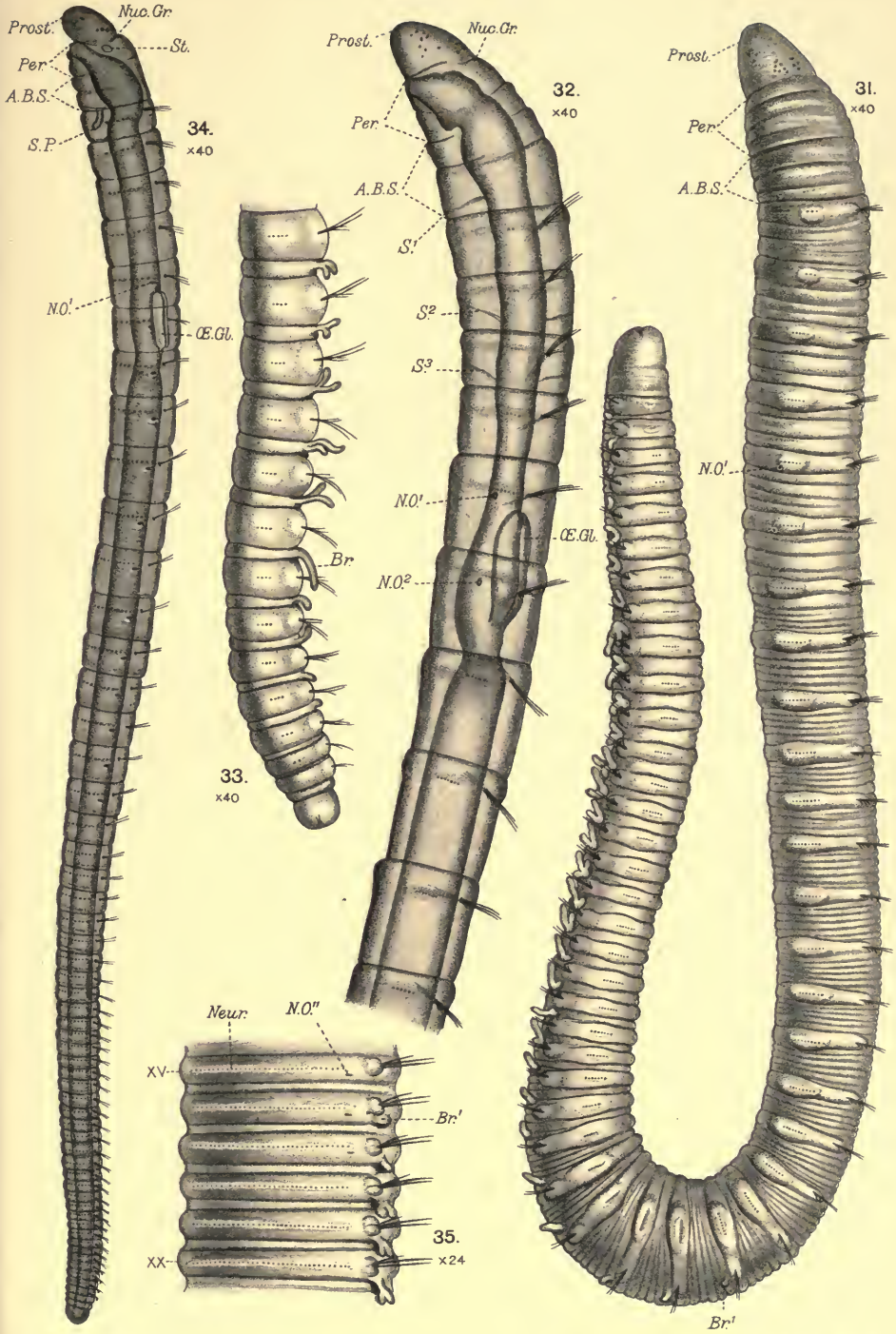


30. x30.

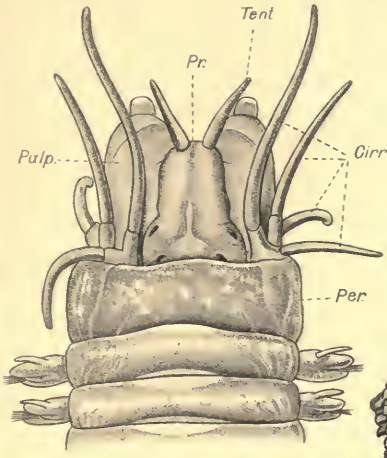
J.H.Ashworth and A.K.Maxwell del.

E.Wilson, Cambridge.

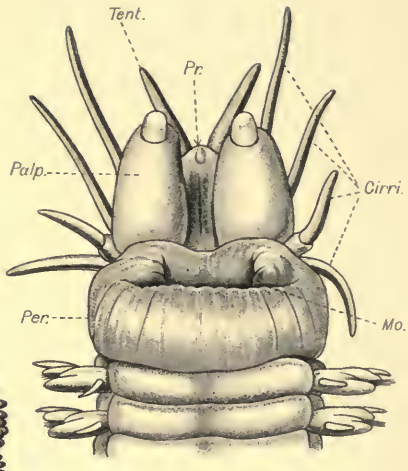


A.K.Maxwell, del.

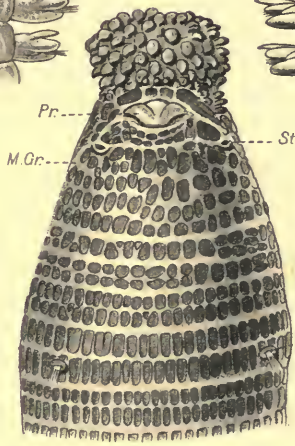
E. Wilson, Cambridge.



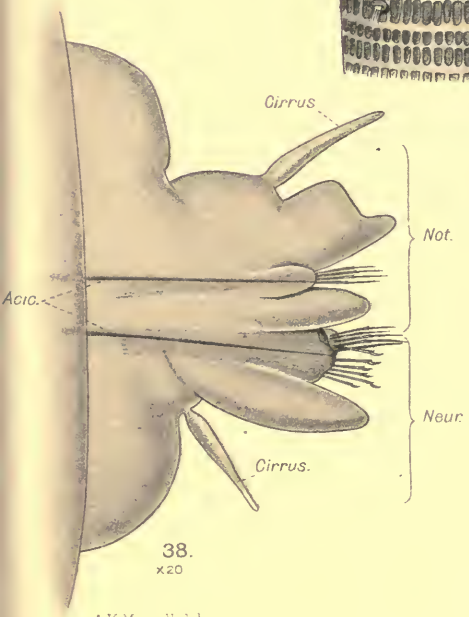
36.
×8



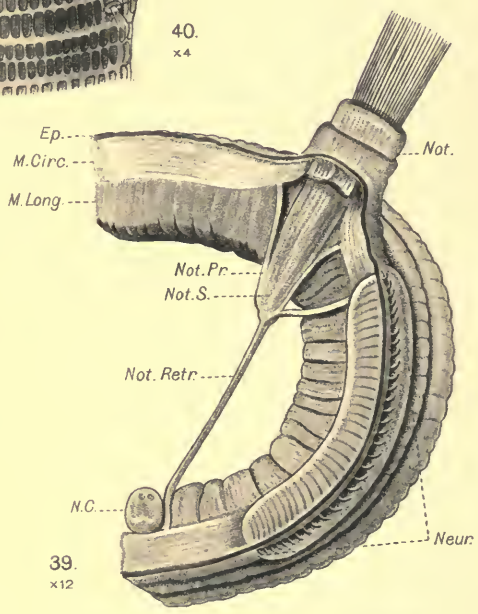
37.
×8



40.
×4



38.
×20



39.
×12

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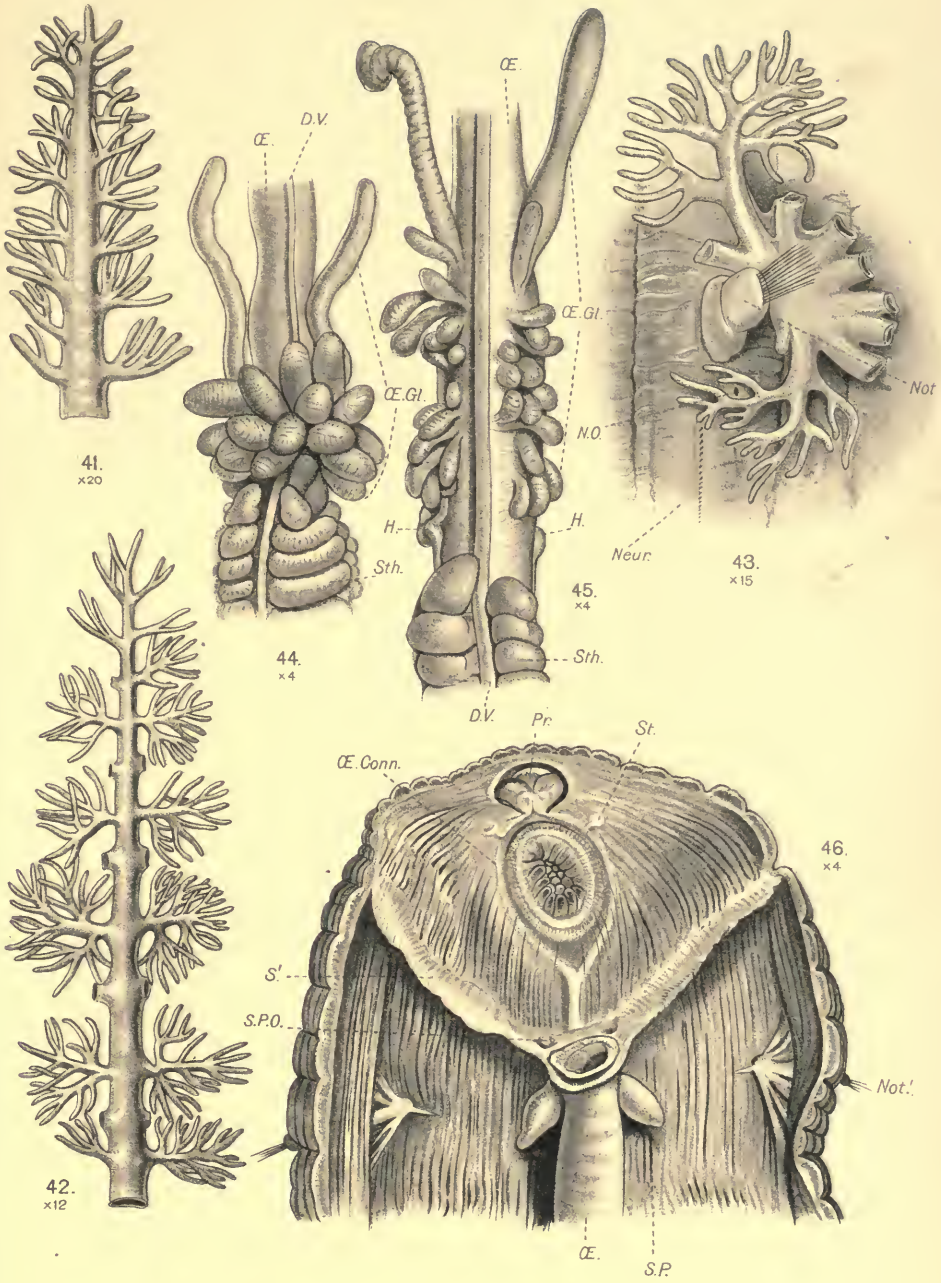

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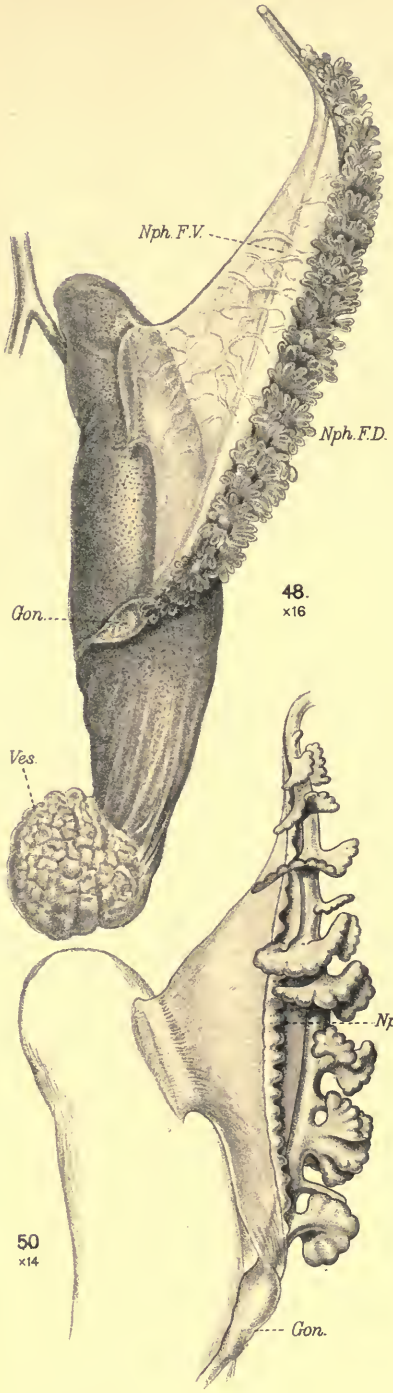

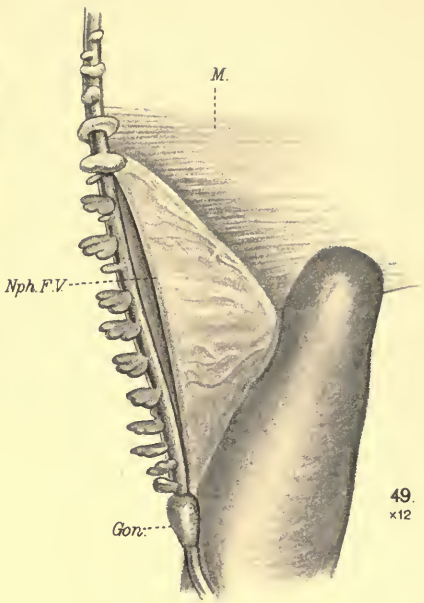

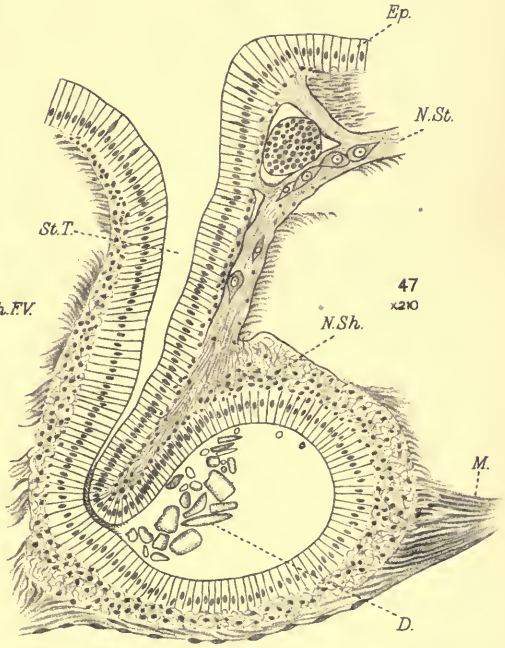

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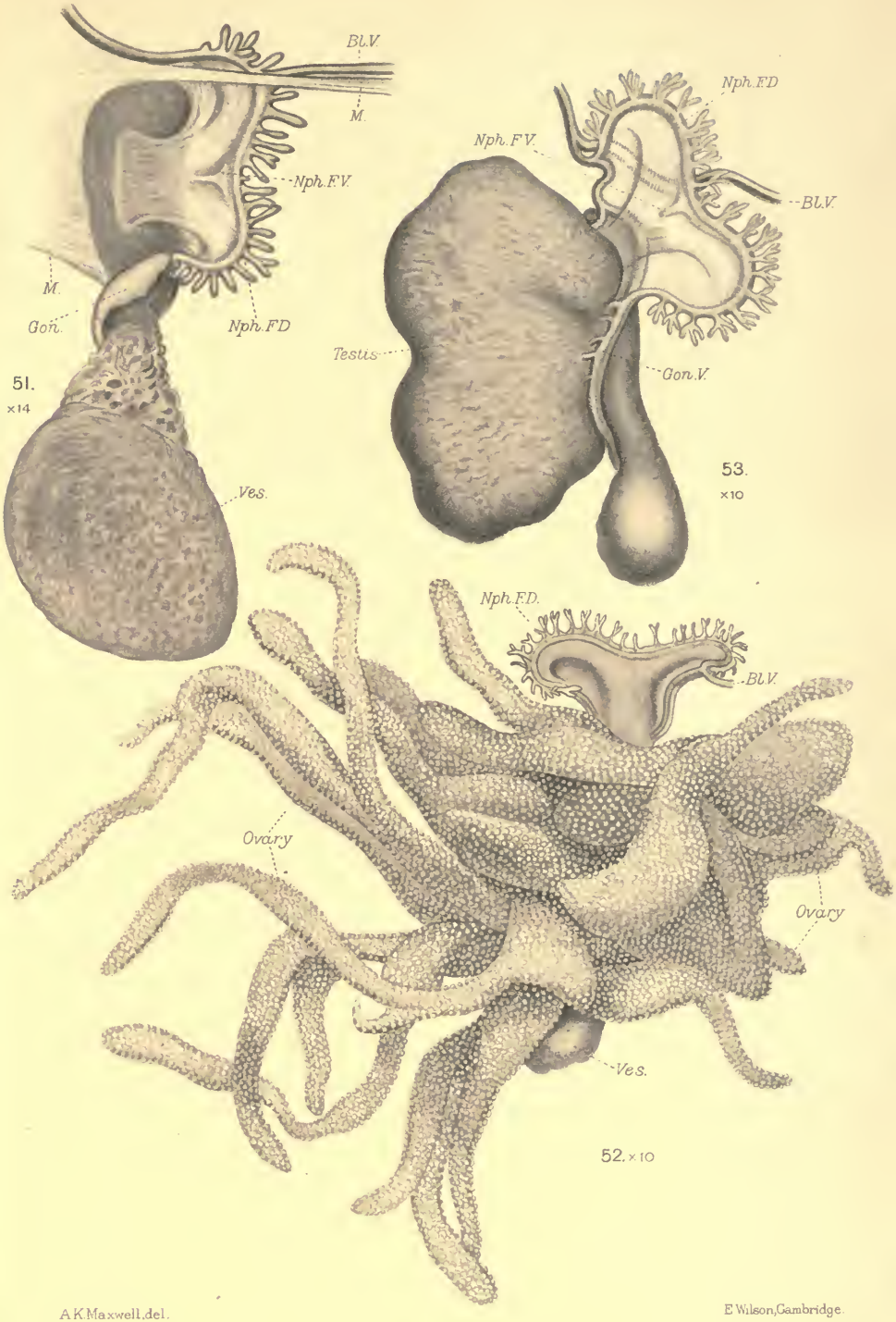

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